

FOSSIL MAMMALS OF AFRICA: 19
THE MIOCENE CARNIVORA OF EAST AFRICA



BY

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A handwritten signature in dark ink, appearing to read "R. J. G. Savage", written over the printed name and affiliation.

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FOSSIL MAMMALS OF AFRICA: 19 THE MIOCENE CARNIVORA OF EAST AFRICA

By R. J. G. SAVAGE

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SYNOPSIS

Eighteen species of carnivores are described from the Tertiary lacustrine tuffs of East Africa, mostly from the Kavirondo Gulf in Kenya and the Napak region in Uganda.

Six of the twelve genera (*Kelba*, *Teratodon*, *Anasinopa*, *Leakitherium*, *Hecubides* and *Kichechia*) and fifteen species are new. *Kelba* is referred to the Arctocyonidae and *Teratodon* is placed in a new family of oxyaenoid creodonts. *Anasinopa*, *Metasinopa*, *Dissopsalis*, *Metapterodon*, *Pterodon*, *Leakitherium* and *Hyaenodon* are all included in the Hyaenodontidae. *Hecubides*, an amphicyonine canid, *Kichechia*, a viverrid, and a species of the felid *Metailurus* are also described. Conclusions on the age of the deposits based on the carnivores, other mammalian elements and radiometric dating converge on Lower Miocene (Burdigalian), with some sites of probable Middle or Upper Miocene (Vindobonian or Pontian) age.

I. INTRODUCTION AND ACKNOWLEDGMENTS

IN the first publication of *Fossil Mammals of Africa* Clark & Leakey (1951) gave an account of the discovery of Miocene fossils in Kenya, listed the sites in the Kavirondo and recorded the fauna as then known. They discussed the probable age of the deposits, based on the known range of mammalian genera recognised in the sequence. Two of the genera used were carnivores, referred to then as *Amphicyon* and *Pseudaelurus*. They concluded that the most probable age for the fauna was Lower Miocene.

Whitworth (1954) in a later publication gave a brief account of the stratigraphy on Rusinga Island, together with a location map of sites.

Accounts of the Tertiary geology of the Kavirondo are to be found in Kent (1944), Shackleton (1951), Whitworth (1953, 1961), Bishop & Whyte (1962) and Bishop (1963).

The mammal faunas from the Kavirondo pyroclastic deposits are extremely rich. The insectivores, bats, primates, lagomorphs, tubulidentates, hyracoids, anthracotheres and ruminants have already been monographed. With the publication of detailed studies on the flora by Chesters (1957) and on the mollusca by Verdcourt (1963), the basis exists for profitable studies on the palaeoecology.

Fifteen out of the eighteen species of carnivore described below are new, six out of the twelve genera are new and there is one new family. This measure emphasises the novelty of the fauna, whose age equivalent is little known elsewhere on the African continent.

Specimens quoted in the text are mostly in the collections of the British Museum (Natural History) and the National Museum of Kenya, Nairobi; their registration numbers are prefaced respectively by the initial letters M. and CMF. Occasional specimens from other institutions are referred to and these named in full in the text. Throughout the systematic description no reference is made to horizon, since the conclusions on stratigraphic age depend on identification of the faunal elements. The subject is dealt with in the final discussion.

My thanks are extended to Dr. L. S. B. Leakey who generously offered me the carnivores for detailed study and kindly arranged for me to spend a field season in Kenya visiting the Kavirondo sites and collecting on Mfanganu Island. Dr. W. Bishop has kindly allowed me to study the Uganda carnivores.

My thanks are also due to Dr. E. I. White and his predecessor as Keeper, the late Mr. W. N. Edwards, for facilities at the British Museum (Natural History).

For advice, criticism and discussion I am indebted to Dr. W. W. Bishop, Professor P. M. Butler, Dr. A. T. Hopwood and Dr. T. Whitworth. Mrs. Shirley Coryndon's careful and painstaking numbering and cataloguing of the Kavirondo fossils has been quite invaluable. Mr. D. Erasmus is responsible for the drawings, excepting Nos. 2, 6-8, 41-43, 47-49 which are by the author. To Mr. E. W. Seavill and Mr. R. Godwin of Bristol University I am indebted for the photography.

II. SYSTEMATIC DESCRIPTIONS

Order CARNIVORA Bowdich

Suborder CREODONTA Cope

Superfamily ARCTOCYONOIDEA Trouessart

Family ARCTOCYONIDAE Murray

DIAGNOSIS. Creodonta with teeth primitive, tritubercular, varying towards sectorial or bunodont. No carnassials or specialised shearing teeth. Premolars mostly simple, acute, an inner cusp on P^4 , sometimes on P^3 and P_4 ; canines large, acute, incisors small. Skull moderately long, brain-case small, sagittal and occipital crests strong, occiput narrow and high, tympanic bulla not ossified. [after Matthew 1937].

REMARKS. Matthew's last revision (1937) is still the basis for arctocyonid studies. Simpson (1945) differed from Matthew in only one detail; Matthew distinguished four subfamilies, namely Oxyclaeninae, Chriacinae, Arctocyoninae and Triisodontinae, while Simpson does not recognise the Chriacinae as sufficiently distinct to merit subfamilial rank; Simpson's interpretation is followed here and the Chriacinae are included with the Oxyclaeninae. The remaining two subfamilies are small, comprising only seven genera. Simpson lists a further four genera which he places in the Arctocyonoidae *incertae sedis*, and to these may now be added *Opsiclaenodon* (Butler 1947) and from them we may subtract *Paroxyclaenus* (Russell & McKenna 1961).

Subfamily OXYCLAENINAE Matthew

DIAGNOSIS. Molars tritubercular, sectorial or bunodont, hypocone rudimentary or distinct; paraconid distinct; premolars simple save sometimes fourth.

REMARKS. The inexactness of the diagnosis emphasises the arbitrary status of the subfamily. It comprises several little known groups and as it stands represents the best solution to the problem of affinity. The Arctocyoninae are distinguishable by their quadrate bunodont molars which have well developed hypocone; the Triisodontinae have round conical cusps on tritubercular molars, the hypocone is weak and the paracone and metacone are progressively connate. Among the *incertae sedis* genera none displays any features which would suggest affinity with the new genus described below.

The Oxycloeninae as defined comprise 15 genera, 14 listed in Simpson (1945) plus *Colpoclaenus* Patterson & McGrew (1962). All are restricted to the Palaeocene and Lower Eocene of North America save *Arctocyonides* which occurs in the Upper Palaeocene of Europe. In three genera, *Carcinodon*, *Prothryptacodon*, and *Spanoxyodon*, no upper dentition is known.

Genus **KELBA** nov.

DIAGNOSIS. Upper molars tritubercular; paracone and metacone equal sized, conical but not connate, parastyle prominent; protocone V-shaped with paraconule and metaconule; cingulum continuous all round, carrying distinct hypocone.

TYPE SPECIES. *Kelba quadeemae* sp. nov.

Kelba quadeemae gen. et sp. nov.

(Pl. 1, fig. 1; Text-figs. 1, 2)

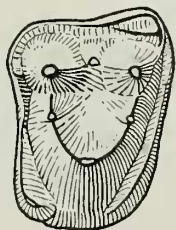
DIAGNOSIS. This is the only known species and the diagnosis is the same as that for the genus. The name is derived from the Arabic *kelb* meaning dog and *quadeem* meaning ancient.

HOLOTYPE. M.19087. Isolated right upper molar, probably M².

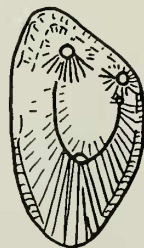
LOCALITY. The holotype is from Rusinga Island, Kavirondo Gulf, Kenya.

ADDITIONAL MATERIAL. In addition to the holotype there is an isolated left upper molar from Mfwanganu Island, Kavirondo Gulf, Kenya, and another molar from Napak in Uganda.

DESCRIPTION. The holotype is an isolated right upper molar, probably M². The tooth is little worn and all details are clearly seen; the outline is quadrate and slightly asymmetrical due to the development of parastyle and hypocone on opposite corners. The paracone and metacone are equally low cones, separated by a vestigial mesostyle; the large protocone is V-shaped, its apex equal in height to the paracone and metacone; the arms of the V carry distinct metaconule and paraconule; the cingulum is continuous round all sides, though not equally developed throughout; it carries a low parastyle and low hypocone and is expanded slightly on the anterior and posterior margins, while being retracted lingually. The tooth is three-rooted, the



1



2

FIGS. 1, 2. *Kelba quadeemae* gen. et sp. nov. (1) Right M². Holotype (M.19087), Rusinga Is. (2) Left M³. (M.19095), Napak. $\times 3$.

root below the protocone being much larger than those below the paracone and metacone.

The second specimen (CMF.4028) from Mfwanganu is a left upper molar, also probably M^2 , and not so well preserved as the holotype. The teeth are similar in size but show slight differences in detail. In the Mfwanganu molar the cingulum is slightly more expanded anteriorly and posteriorly, and the mesostyle slightly more prominent.

An isolated upper molar, (M.19095) from Napak IV in Uganda is also referred to the species. This tooth is probably a left M^3 , transversely elongated, with width almost twice the antero-posterior length: the protocone is a large V-shaped cusp, the paracone rises to the same height as the protocone and the metacone is very small; a cingulum is developed on either side of the protocone and anterobucally to the paracone. The three roots are situated below the paracone, protocone and metacone; the protocone root is the largest and the metacone root very small.

REMARKS. Isolated molars with a basic tribosphenic pattern such as the teeth described above are very difficult to identify with certainty. At this level of organisation there is extremely little difference between the teeth of insectivores, primates, tillodonts, creodonts, condylarths, pantodonts and dichobunodonts. Beyond the superficial similarity of these groups, the closest structural resemblances to *Kelba* are to be found among species usually referred to creodonts or condylarths. The condylarths were examined carefully and the case for the inclusion of *Kelba* there was found rather less convincing than with the creodonts. Among the Condylarthra, the Phenacodontidae lack a well developed V-shaped protocone, the Peripitychidae possess more or less symmetrical hypocone and ectocone, and the Meniscotheriidae tend towards lophodont molars. Among the Hyopsodontidae, the Hyopsodontinae are all small insectivorous mammals with sexi-tubercular molars and the Mioclaeninae have tritubercular molars which either lack or have a rudimentary hypocone. Although *Kelba* is thus placed here among the Arctocyoniidae, it will be necessary when more material is available to review this assessment.

The differences between the two specimens of M^2 are so slight, and in view of the proximity of Mfwanganu and Rusinga, there seems little doubt they belong to the same species.

The new record extends the range of the arctocyonids to Africa. Most of our knowledge of the group is based on North American finds, and surprisingly the new species shows no close affinity to either the known European or Asian arctocyonids. Affinity is greatest with the Oxyclaeninae, and in particular close similarities can be seen with *Metachriacus*, *Deltatherium*, *Tricentes* and *Loxolophus*; these genera all occur in the Palaeocene of North America, the first three in the Middle and the last in the Lower Palaeocene. In *Deltatherium* the molars are more sectorial and less bunodont, the mesostyle is undeveloped and the cingulum extends lingually beyond the protocone. In *Metachriacus* the upper dentition is not fully known (M^2 in the only specimen with molars is broken lingually), but enough is available to make a close comparison. *Metachriacus* molars lack a parastyle, the paracone is slightly larger than the metacone, and in M^1 and possibly M^2 the protocone is asymmetrical;

otherwise the dentition is similar to the new genus. The closest affinities to *Kelba* are probably to be found in *Tricentes*; this genus with *Loxolophus* has few features which vary from *Kelba*. Both Palaeocene genera have bunodont molars, the paracone is rather larger than the metacone, and a small parastyle is present. In *Loxolophus* the cingulum extends more lingually than in *Tricentes*.

The four American genera mentioned above differ from each other as greatly as they differ from *Kelba*. No clear ancestry for *Kelba* is obvious among the Palaeocene forms; on the whole *Tricentes* is perhaps closer than any of the others. *Kelba* would appear to represent a late survivor of a primitive stock, as probably are *Didymoconus* and *Ardynictis*, two genera of arctocyonids described by Matthew & Granger (1924, 1925) from the Lower Oligocene of Mongolia.

Measurements (in mm.) for *Kelba quadeemae*

	M ² M.19087 Holotype	M ² CMF.4028	M ³ M.19095
Ant-post.	10.2	9.6	7.1
trs.	12.3	12.2	11.7

Superfamily **OXYAENOIDEA** Osborn 1910

Family **TERATODONTIDAE** nov.

DIAGNOSIS. M₃² present; M³ transverse; M₃² main carnassial, M₁¹ less functional as carnassial. Premolars large, bunodont, tubercular with thick enamel: P⁴ larger than M¹. Lower molars with small talonid and metaconid present; M₂ larger than M₁. Jaw relatively short.

REMARKS. The superfamily Oxyaenoidea Osborn 1910 is synonymous with Pseudocreoedi Matthew 1909, Osborn's name having validity. The superfamily comprises only two families, Oxyaenidae and Hyaenodontidae, to which is here added a third. In the Oxyaenidae M₃² are absent in all known genera, M² is transverse and M₁¹ are the functional carnassials: the premolars may enlarge and P³ has progressively developed protocone: the jaw is short and the symphysis robust. The Hyaenodontidae is a much less compact family: in all genera P³ lacks a distinct protocone. Within the Hyaenodontidae are four subfamilies: the Limnocyoninae and Machaeroidinae lack M³ and M² is always transverse, (*Prolimnocyon* is the one exception—M² is transverse and a vestigial M³ is present): Hyaenodontinae lacks metaconid on lower molars: Proviverrivinae retains M³ and metaconid on lower molars, the skull is narrow and jaws long. Gazin (1946) proposed that the Limnocyoninae and Machaeroidinae be given family recognition as the Limnocyonidae. As our concern here is with the Hyaenodontidae *sensu stricto* we shall not pursue the wrangle. Clearly the status of the Creodonta as we know them today is measured; arctocyonids and hyaenodontids are likely to be among the first victims.

Most of the known characters of the Teratodontidae can be found within the subfamilies of the Oxyaenidae and Hyaenodontidae, but the combination is unique to the Teratodontidae. In particular the extraordinary premolars mark out the teratodontids from all oxyaenids and hyaenodontids.

The new family is established to accommodate two species of *Teratodon* gen. nov. described below and in addition I would transfer to the family *Quercytherium tenebrosus* Filhol from the Upper Eocene—Middle Oligocene of France.

Genus **TERATODON** nov.

DIAGNOSIS. Teratodontid of medium size, jaws relatively short. M^1 and M^2 metacone slightly larger than and connate with paracone; elongate metastyle; M^2 slightly larger than M^1 . P^4 bitubercular and larger than M^1 ; protocone almost as large as paracone. Lower molars with well developed metaconid, trigonid cusps high, talonid small, paraconid-protoconid shear very oblique. P_3 large with low single cusp.

Generic name derived from the Greek *teras*, a monster or strange creature and *odous* a tooth.

TYPE SPECIES. *Teratodon spekei* sp. nov.

SPECIES AND DISTRIBUTION. The type species is known from Koru and Songhor. There is in addition a second species from Songhor described below.

Teratodon spekei gen. et sp. nov.

(Pl. I, figs. 2, 3; Text-figs. 3–11)

DIAGNOSIS. Species about size of *Vulpes vulpes*; metastyle on M^2 elongate transversely but not extending beyond the level of the parastyle.

The trivial name is in memory of Captain John Hanning Speke of Dowlish Wake, Somerset, who in 1859 discovered Lake Victoria.

HOLOTYPE. M.14307. Left maxilla with P^4 , M^{1+2} and alveolus of M^3 ; from Koru near Kavirondo Gulf, Lake Victoria, Kenya.

ADDITIONAL MATERIAL. In addition to the holotype, the type locality has yielded the following additional specimens:

M.14215. Right maxilla with P^4 and M^2 and broken root of M^1 . (Paratype)

M.14310. Anterior maxillae with canine and P^2 on both sides and alveoli of P^1 . (Paratype).

[These two specimens probably belong to the same individual as the holotype.]

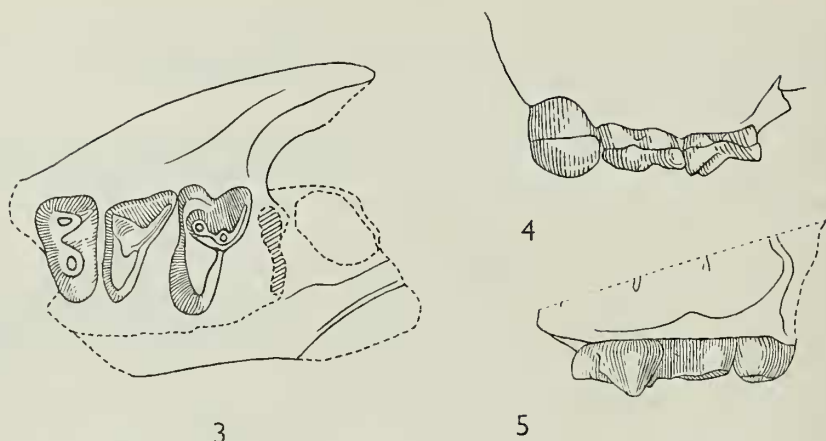
M.14216. Left mandibular fragment with M_2 and M_3 .

M.14308. Right mandibular fragment, symphyseal region with two very worn premolars and part of a third.

The following two specimens from the type locality are referred to the species:

M.14204. Mandible fragment with very worn premolar and root of another premolar.

M.14225. Right lower canine.



FIGS. 3-5. *Teratodon spekei* gen. et sp. nov. Left maxilla with P^4 , M^1 , M^2 . (3) Occlusal aspect. (4) Lateral aspect. (5) Medial aspect. Holotype (M.14307), Koru. $\times 2$.

Songhor, a site about 10 miles NW of Koru, has yielded the following mandibular remains:

CMF.4039. Right mandible with DP_3 , P_2 , M_{1+2} , and unerupted M_3 .

CMF.4040. Left mandible with M_{1+2} , and unerupted M_3 .

[These two specimens probably belong to the same individual.]

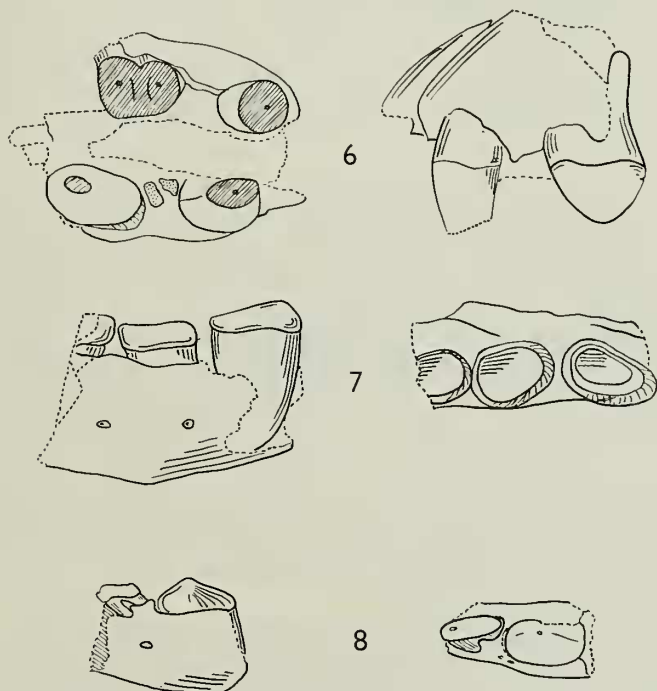
CMF.4041. Left mandibular fragment with P_{1+2} .

DESCRIPTION. The holotype comprises a posterior maxillary fragment with the anterior part of the jugal arch, P^4 , M^{1+2} in place and the alveolus of M^3 : attached to the specimen is a piece of frontal bone showing the anterior line of the temporal muscle origin. The strength of the jugal arch and the depth of the temporal insertion (together with the robustness of the mandible) suggest a strongly built skull with massive temporal muscles. The right maxilla, M.14215, probably belongs to the same individual as the holotype; they come from the same site, are the same size and have the same degree of wear on the teeth. The anterior fragment of maxilla M.14310 may also belong to this individual.

M^1 and M^2 are closely similar, M^2 being slightly larger than M^1 . On the paratype little more than the roots of M^1 remain, while on the holotype the crown of M^1 is rather worn; but from what can be seen, it does not differ structurally from M^2 . M^2 has low connate paracone and metacone, small parastyle and metastyle which is elongated transversely; the metacone is larger than the paracone; the protocone is V-shaped and attenuated transversely. The alveolus for M^3 extends transversely across the palate as far as that of M^2 , and this evidence taken with the fully developed M_3 indicates a sizeable transverse tooth.

P^4 is startlingly different from the molars; it is present in both holotype and paratype. The tooth is massive and robust, with two thick roots and the crown surface area is slightly greater than that of M^1 . The enamel is thick and although in both specimens the cusps are worn flat, the bases of two cusps are recognizable; these must have been low tubercular cusps. P^3 is unknown though presumably present.

P^2 is an extremely stout tooth with two strong roots; the crown forms a low symmetrical ovate cone, with slight ridge near the base on the antero-lateral side and suggestion of a cingulum on the posterior margin. P^1 was very much reduced and double rooted; it would appear that the size relationships between P^1 and P^2 were similar to those between P_1 and P_2 described below. The upper canine is well but not strongly developed; the antero-posterior diameter at the base of the crown is much less than that on P^2 . The canine is flattened laterally, more so on the inner side with anterior and posterior keels. The tip is not preserved and no trace of a saw-edge is evident on the proximal parts of the tooth. The premaxillae are missing though fragments of the nasals survive.



FIGS. 6-8. *Teratodon spekei*. (6) Maxillae with canines and P^2 , occlusal and lateral aspects. (M.14310), Koru. (7) Right mandible with P_2 , occlusal and lateral aspects. (M.14308), Koru. (8) Left mandible with P_1 , occlusal and lateral aspects. (CMF.4041), Songhor. All $\times 1.5$.

Material of the lower dentition is more abundant and between the specimens almost a complete dentition is known. Specimens CMF.4039, 4040 and 4041 probably all belong to the same individual, while specimens M.14308 and M.14216 probably belong to another individual which could well be the same as the holotype, M.14215 and M.14310. The Songhor individual is immature with the permanent dentition still erupting while the Koru animal is a fully mature adult with well worn dentition.

Of the three molars, M_1 is the smallest and M_3 the largest, and all three are

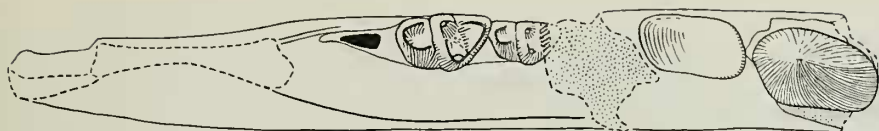
basically similar. M_2 has a high pointed trigonid, the paraconid-protoconid cusps are about equally high and form an oblique shearing blade; the metaconid is small and a stud is present on the cingulum below the shearing edge of the paraconid: the talonid is slightly shorter than the trigonid and it faces steeply downward and inward from a high buccal wall to the low lingual edge. In the adult specimen (M.14216) M_2 trigonid cusps are worn flat from grinding. M_1 on the two juvenile jaws (CMF. 4039 and 4040) is similar to M_2 , but smaller; the trigonid is worn flat making ineffective the shearing paraconid-protoconid edge; the paraconid-protoconid edge is less obliquely inclined. M_3 , fully erupted on M.14216, has a trigonid which is rather bigger than that of M_2 although the talonid is no larger; the high paraconid-protocnid shearing blade shows it to be the main carnassial, occluding with M^2 . In the juvenile jaws the unerupted M_3 can be clearly seen in X-ray photographs and in both specimens the bone is just opened so that the tip of the protoconid is visible. On specimen M.14216 only M_{2+3} are preserved, together with the posterior root of M_1 : the jaw is remarkably robust for the size of the teeth, being thick in proportion to its depth.

Mandible CMF.4040 is not preserved anterior to M_1 . Specimen CMF.4039 is preserved up to and including the symphysis: the coronoid process and condyloid articulation are missing, as is the tip of the angular process. The body of the mandible is slender, relatively short and the symphysis large: the symphyseal area is rough and D-shaped. A mental foramen is present on the lateral border behind P_2 . The two teeth preserved anterior to the molars are taken to be fully erupted and worn DP_3 and P_2 erupting: P_4 would have formed in jaw cavity between DP_3 and M_1 . DP_3 is as large as M_2 ; it has two roots, but the crown is worn flat almost to the base and no details can be discerned. P_2 is just erupting above the symphysis and is much the largest tooth in the series: it is oval with two roots, with thick enamel on crown which forms a massive but very low pointed cusp. Between the anterior root of P_2 and the symphysis is a small cavity, probably for the canine root tip. In the large cavity within the mandible between M_1 and DP_3 was an undeveloped tooth; only a single cusp tip is calcified and nothing further can be traced; it is presumed that this tooth is the developing P_4 .

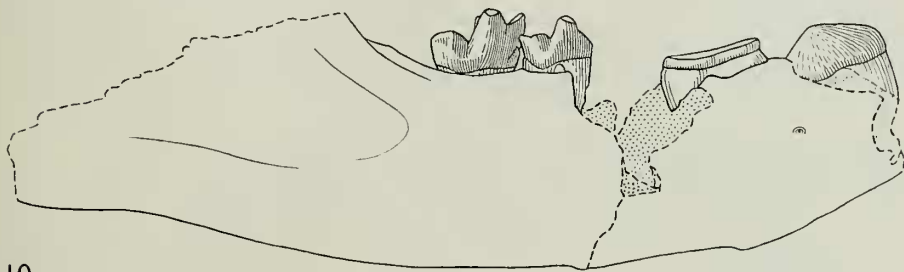
Specimen CMF.4041 preserves P_{1+2} around the symphyseal region; P_2 is identical to that in CMF.4039 and is also just erupting through the bone. P_1 is preserved on the left side, a small laterally compressed two rooted tooth with low anteriorly placed cusp. Specimen M.14308 from the type locality has two very worn premolars preserved, taken to be P_2 and P_3 , on basis of size and position in mandible relative to symphysis and mental foramina; the anterior half of P_4 also survives and is again worn almost to the base of the crown. This robust mandible fragment could belong to the same individual as M.14216 and the holotype.

M.14204 has very worn premolar preserved, probably P_3 , and behind it the roots of P_4 . M.14225 is an isolated canine from Koru, ovate and more compressed on the inner side, curved more strongly than the upper described; it is of the size and shape expected of a lower canine of *T. spekei*.

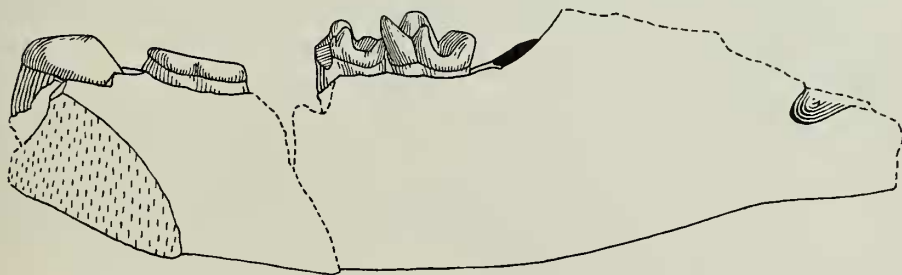
REMARKS. The premolars are the outstanding feature of *Teratodon*. No other



9



10



11

FIGS. 9-11. *Teratodon spekei*. Right mandible with DP_3 , P_2 , M_1 2. (9) Occlusal aspect. (10) Lateral aspect. (11) Medial aspect. (CMF.4039), Songhor. $\times 1.5$.

carnivore or carnivorous mammal known to me has quite such an extraordinary combination of premolars and molars. Their highly exceptional character, seen in the maxillae and mandibles from Koru and the mandibles from Songhor makes the linkage between these two sites (about 10 miles apart) plausible. Associated with the bunodont premolars is the robust build of the jaws and their heavy musculature.

The functioning of this dentition presents ocusal and mechanical problems. M_3^2 are clearly the main carnassial teeth, both on basis of structure and wear. The blades are high, but their obliqueness may be regarded as a primitive feature. Anterior to these come the grinding premolars: the wear surfaces on the upper premolars are almost flat and directed slightly dorsally and anteriorly; there is little definite trace of direction of movement on the surface, but from faint striations it would appear more likely to have been transverse than longitudinal. Unfortunately

the condyloid process is unknown and hence we are ignorant of any articular modifications. It is difficult, from a purely mechanical viewpoint, to see how a typical carnivore can perform efficiently the dual function of shearing at the back and grinding anterior to this: the molars seem likely to impede grinding movements. Both processes require powerful movements, best achieved with the occlusal surfaces near the fulcrum and a long moment arm from the fulcrum to the line of action of the muscles (temporal and masseter mainly). The flattened surface of M^1 and the trace of wear on the cusps of M^2 suggest the molars are inevitably occluded during pre-molar grinding. The premolars could only grind if their height carried them above the level of the molars; height alone would be useless and must be accompanied by thickened enamel or more complex tooth structure if it is not to be rapidly lost. *Teratodon* premolars are large and have thick enamel.

The only fossil material with which comparison can usefully be made is *Quercytherium* from the Upper Eocene of Phosphorites du Quercy and Gard in France. Here too can be seen the enlarged premolars, the second being the largest in the series. Piveteau (1961) has suggested that the specialized dentition of *Quercytherium* can be compared with that of hyaenids. The anatomical comparison does not stand up to detailed examination but functionally there is parallelism in that both combine crushing and shearing teeth.

In my osteological collection I have a dog skull from Ounianga Kebir, an inhabited oasis in the midst of the Sahara desert. This skull illustrates what can happen to a typical carnivore when forced to feed very largely on vegetable material. The people of the oasis live largely on a diet of rice and dates, with occasional goat and chicken on festive occasions. The dogs subsist largely on dates, and these mostly rejects too sandy for human consumption. In the desert without the utmost care, sand covers all food near ground level: the combination of sand and date stones soon wears down teeth. On this particular dog skull, all the premolars and molars are worn to flat surfaces, the M^3 no less than P^2 : only the outer rim of P^4 remains rather above the levelled dentition. Further, these teeth show well marked transverse striations indicating lateral grinding movement.

The feeding habits of *Teratodon* remain something of a mystery. The premolar structure shows a departure from normal and the feeding habits appear to make use of these modifications. The dentition as a whole seems unbalanced, and far from being a satisfactory compromise, it seems to get the worst of both: the carnassials cannot function efficiently because of the large premolars and the premolars cannot grind efficiently because of their position and the presence of shearing molars behind. The jaw movements were probably not dissimilar to those of the Ounianga dog. Instead of desert sand and date stones, we can imagine volcanic dust and stones of the savannah fruits (well fossilized on Rusinga, see Chesters 1957).

A small stud at the base of the paraconid on the lower molars has been described. It cannot occlude with anything as it is too low, yet it is very well developed on M_2 and M_3 , though less so on M_1 . I suggest the stud acted as a guide to erupting teeth, keeping them in true alignment: if the carnassials erupt with lateral displacement, the blades will not shear: so long as the posterior edge of the proceeding molar is

medial to the stud, then the shear should function. *Teratodon* was probably quite vulnerable to displaced eruptions owing to the shortened jaw.

AFFINITIES. The classification of *Teratodon* presents difficulties: on the basis of the molars alone, it is clearly to be numbered among the Proviverrinae; but the premolar specialities and associated shortening of the jaws rule this out. Enlarged premolars are not uncommon in the Oxyaenidae and are to be found in some of the carnivorous marsupials, Borhyaenidae: the differences in molar structure, however, rule out possibility of affinity with these families and the expanded premolars reflect homeomorphy.

The molar teeth of *Teratodon* are comparable with those of *Anasinopa* described below and with *Sinopa*. *Anasinopa* is much larger and the shear on the carnassials less oblique; *Sinopa* is intermediate between the other two.

	M ² Angle between shear and paracone-metacone line	M ₃ Angle between shear and paraconid-metaconid line
<i>Teratodon</i>	80°	50°
<i>Sinopa</i>	60°	45°
<i>Anasinopa</i>	50°	40°

The Teratodontids could be regarded as an early offshoot of the Oxyaenoidea, close to the Proviverrinae, retaining M³ and molars with very oblique shear, while specializing in the development of crushing premolars.

TABLE I
Measurements (in mm.) for *Teratodon spekei*

		C	P ²	P ⁴	M ¹	M ²	P ₁	P ₂	P ₃	M ₁	M ₂	M ₃
M.14310	a-p	9.1	12.9									
	trs	5.7	8.3									
M.14307	a-p			6.7	6.8	6.8						
Holotype	trs			9.5	9.5	10.7						
M.14215	a-p			6.5		6.7						
	trs			9.8		11.0						
M.14216	a-p										7.3	9.4
	trs										5.0	6.3
M.14308	a-p							12.6	10.8			
	trs							7.4	8.8			
CMF.4039	a-p							11.5*	9.0D	—	7.4	
	trs							6.5	4.9	3.8	5.1	
CMF.4040	a-p									6.0	7.3	
	trs									3.8	4.9	
CMF.4041	a-p						6.9	11.2				
	trs						2.7	7.0				

*Tooth erupting; measurement approximate. D, Deciduous premolar, probably DP₃

Teratodon enigmae sp. nov.

(Pl. I figs. 4, 5; Text-figs. 12-18)

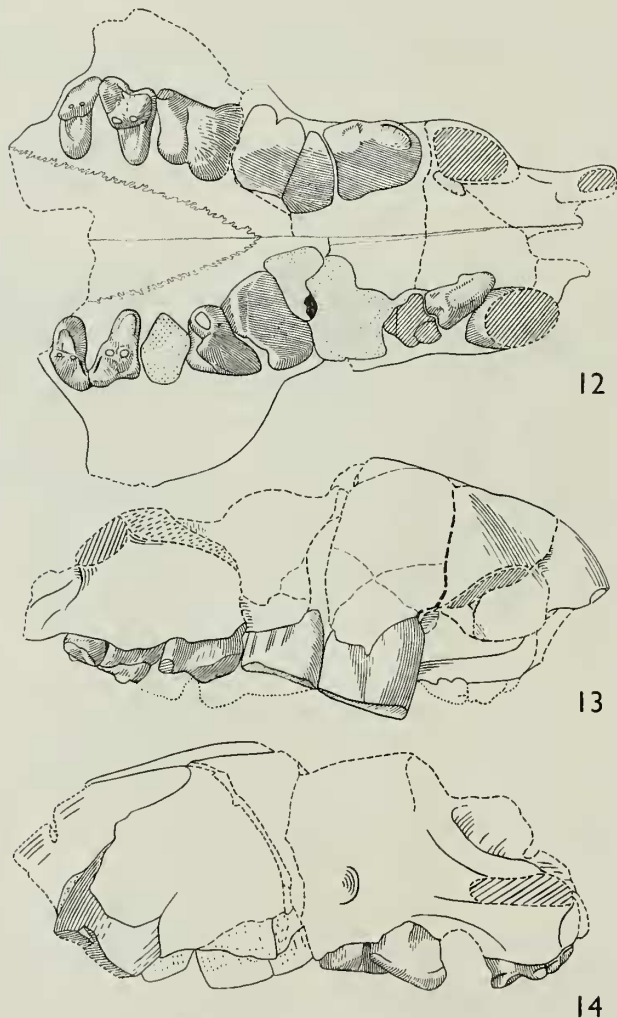
DIAGNOSIS. Differs from the type species in having shorter and more robust jaws,

and very heavy premolars. On M^2 the metastyle extends laterally beyond the level of the parastyle. Both upper and lower canines are large and the snout is blunt.

HOLOTYPE. M.19088. Facial region with dentition fairly complete behind the incisors. From Songhor, near Kavirondo Gulf, Kenya.

ADDITIONAL MATERIAL. A left mandible, M.19089, from the same site and possibly belonging to the same individual as the holotype, is referred to the species.

DESCRIPTION. The holotype comprises a reasonably complete facial region with most of the dentition posterior to the incisors. Maxillae, nasal and palatine bones



FIGS. 12-14. *Teratodon enigmae* sp. nov. Maxillary region. (12) Occlusal aspect. (13) Right lateral aspect. (14) Left lateral aspect. Holotype. (M.19088a), Songhor. $\times 1$.

are preserved and the sutures visible. The complete nasals are entirely horizontal, elongate and with parallel sides: the anterior edge is transverse with a very short lateral arm adjoining the premaxilla. The premaxillae are broken anteriorly, but the root of one incisor remains on the right side; posteriorly they extend back and overlap the nasals for some 15 mm. Between the large root of the upper canine and the premaxillary border of the maxilla is a deep groove, the lower part of which may have accommodated the lower canine. There are in addition fragments of right frontal and parietals, the latter showing high sagittal crest.

The upper molars are similar to *Teratodon spekei* but beyond this close similarity ends. The jaw is short and very much constricted in the premolar region. The mandible and beginning of the jugal arch are heavily built. Other than fractures due to fossilization, the bone is in good condition and shows no sign of fracture during life or any other abnormality. In contrast to this the dentition is bizarre. The beast is presumed to have had three molars, of which M^2 and M^3 are well preserved on both sides. M^2 is distinguishable from that of *Teratodon spekei* only by the more elongate metastyle, which is extended well beyond the level of the parastyle. M^3 is a transverse molar of the size and proportions expected of *Teratodon spekei*: it has V-shaped protocone, connate paracone and metacone, the paracone slightly larger than the metacone, elongated parastyle extending to meet the metastyle of M^2 .

In the short gap between the canine and M^2 is crowded a grotesque array of 'premolars', which almost defy description. These 'teeth', as will be seen from the illustrations, cannot be numbered P^{1-4} ; they possess massive roots, they are not symmetrical on left and right, the crowns are worn into a longitudinal concave arc and are without trace of a cingulum, the largest tooth is midway between the canine and M^2 and is so broad that a palatal gap of only 4 mm. is left.

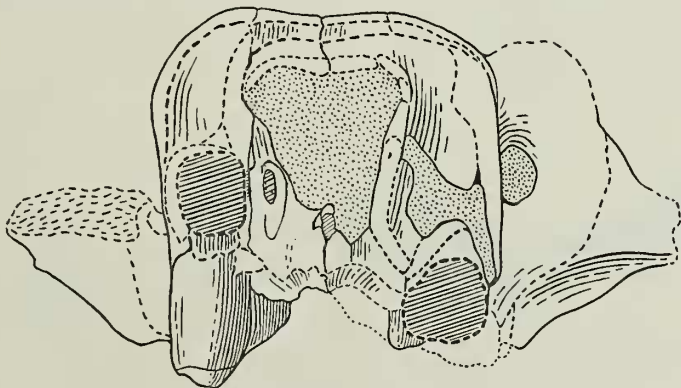
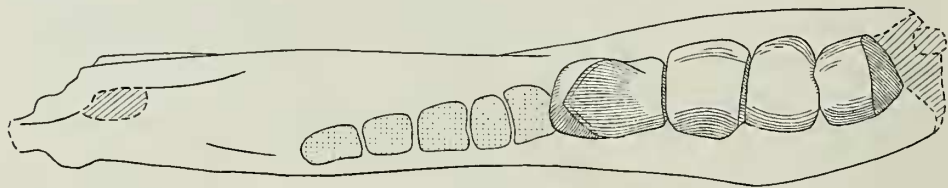


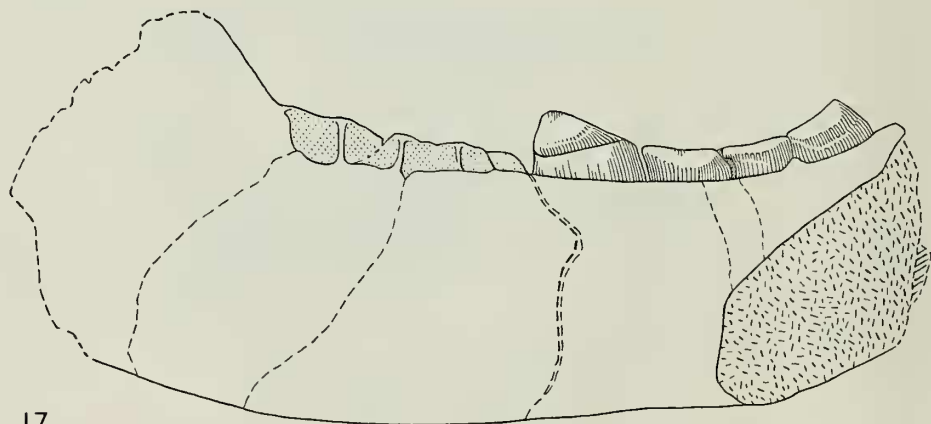
FIG. 15. *Teratodon enigmae*. Maxillary region, anterior aspect. Holotype (M.19088a), Songhor. $\times 1.5$.

The robust mandible has a large symphysis and two mental foramina, the larger and more posterior under $?P_3$. The five alveoli at the back of the mandible presumably are for the three molars, though it is far from clear to see how three teeth, each of which could be expected to have two roots, can fit into five alveoli. The root of the canine is visible beside the symphysis and on its outer edge the root tip of $?P_1$.

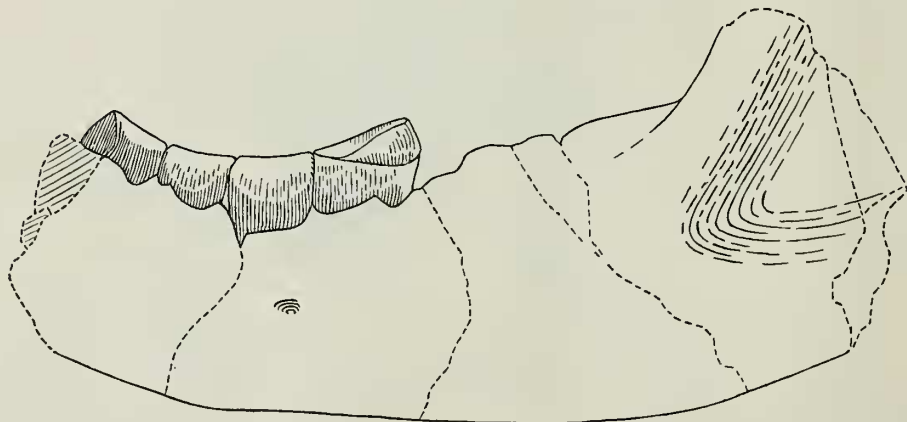
Between this root tip and the molar alveoli are four tooth stumps, so worn that no characters remain: a little enamel is left on the posterior edge of the last of these four teeth: the wear surface forms a longitudinal concave arc as on the upper dentition.



16



17



18

FIGS. 16-18. *Teratodon enigmae*. Left mandible. (16) Occlusal aspect. (17) Medial aspect. (18) Lateral aspect. (M.19089), Songhor. $\times 1.5$.

REMARKS. Although the skull bones are in places broken, the joins are clear and there is no doubt the pieces have been assembled correctly. Hence the possibility that pieces of several individuals, or even several species, being assembled together is ruled out. It seems inconceivable that this individual represents the norm of the species. The predominance of transverse striations on the upper and lower 'premolars', together with the shape of the facets, suggests that these are genuine occlusion facets and not weathering surfaces. It must follow that the specimen is that of an abnormal individual. If the abnormality was caused by damage to the jaw and or tooth germs, then more asymmetry would be expected, and some sign of bone repair inevitable. No pathological cause is known which would produce such bizarre patterns. This leaves only a congenital cause for the abnormality and the individual must be a mutant.

The norm of the species probably represents something quite different from *Teratodon spekei*. The parallel sided nasomaxillary region, expanding rapidly from the springing of the jugals, the flat topped and blunt nosed snout with large maxillo-turbinal cavity, recall proportions seen in *Enhydra*, the sea-otter. The cheek dentition in *Enhydra* is relatively large and the enamel thick—adaptations to shell-crushing. It is tempting to think of *T. enigmae* as a shell-crushing aquatic form, breaking molluscs loose with its strong canines and crushing them with the heavy premolars.

Without insisting that the above reasoning is water-tight and that no other solutions are possible, I submit that on the available evidence it seems the most plausible explanation. It would greatly help to have more material: the population may represent one of those interesting short periods of genetical instability so rarely preserved, when many new prototypes are appearing and disappearing in the process of establishing a few new strains.

Measurements (in mm.) on *Teratodon enigmae* (M.19088a):

		C	M ²	M ³
Right side	a-p	13.2*	7.0	5.3
	trs	7.3*	11.6	10.4
Left side	a-p	13.6	7.1	5.2
	trs	9.2	11.2	10.4

*Measurement taken on root.

Family HYAENODONTIDAE Leidy

DIAGNOSIS. Creodonta with upper molars either three or reduced to two; two front upper molars specialised as carnassial teeth either tuberculo-sectorial or completely sectorial; last upper molar, when present, transversely extended; all the lower molars specialised as carnassial teeth; $P\frac{1}{1}$ two-rooted, except in some specialised genera; primitive forms with long and slender skulls; tail long and heavy; later forms with more robust skull, claws blunt; cursorial adaptations to a varying extent. [after Pilgrim 1932].

REMARKS. The diagnosis omits details of post-cranial characters, to be found in the diagnoses of Matthew (1909) and Denison (1938). The Hyaenodontidae together with the Oxyaenidae make up the superfamily Oxyaenoidea. (=Pseudocredodi of Matthew 1909 and Denison 1938). Of the four subfamilies of Hyaenodontidae,

Denison (1938) grouped together the Limnocyoninae and Machaeroidinae as short broad skulled types, and the Proviverrinae and Hyaenodontinae as long faced narrow skulled types, while Gazin (1946) separated the Limnocyoninae and Machaeroidinae in a new family, the Limnocyonidae.

Subfamily PROVIVERRINAE Matthew

DIAGNOSIS. Hyaenodontidae with narrow skull and long face; M_3^3 ; molars tributercular above, tuberculo-sectorial below; metaconids present on lower molars; carnassial specialization less advanced [After Matthew 1909].

REMARKS. The skull and facial characters distinguish the subfamily from the Limnocyoninae and Machaeroidinae: the tooth characters distinguish it from the Hyaenodontinae. Of the 12 genera comprising the sub-family, 7 of these are listed by Simpson (1945) and four have been added since; Stovall (1948) added *Ischnognathus* and three are due to Matthes (1952), *Prodissopsalis*, *Leonhardtina* and *Geiselotherium*. The Eocene of North America has yielded *Sinopa* and *Tritemnodon*, and from the European Eocene come *Prorhyzaena*, *Proviverra*, *Paracynohyaenodon*, *Prodissopsalis*, *Leonhardtina* and *Geiselotherium*. (Simpson also includes in his list *Cynohyaenodon* and *Galethylax*, both of which I consider synonymous with *Proviverra*). The Oligocene has yielded *Ischnognathus* in North America and *Metasinopa* in Egypt. The only Miocene form is *Dissopsalis* from India. To these is now added a further genus from East Africa.

COMMENT.—Matthes (1952) described a new creodont fauna from the Middle Eocene lignite beds of Geiseltal; the six new proviverrine species described are placed by Matthes in four new genera. Unfortunately the photographic plates have reproduced very poorly and there are no diagrams of the dentitions, hence interpretation is seriously impeded. None of the new species or genera is very close to the new African genus described below, but the taxonomy in the paper calls for some comment. I consider two of the species, *Imperatoria gallwitzi* and *I. hageni* to be identical. Both are known only from mandibles and lower dentitions: they have identical morphological characters and the size differences are so slight that they are well within the range of individual variation, as seen in the following figures (from Matthes 1952):

	<i>I. gallwitzi</i> (mm.)	<i>I. hageni</i>
M_{1-3}	38	40
P_1-M_3	80	85
Length M_1	11	12
„ M_2	13	14
„ M_3	14	14

Imperatoria is known only from mandibles and lower dentitions and *Prodissopsalis* is known only from skulls and maxillary dentitions. Both occur in the same beds at the same sites; both are the same size. The dentition of *Imperatoria* corresponds exactly in composition, pattern and size with that which could be envisaged for the

lower dentition of *Prodissopsalis*, as shown in the following figures where comparison is made with the upper and lower dentition of the closely related genus *Sinopa*.

<i>Sinopa grangeri</i> (Matthew 1906)	a M ¹⁻³ 22.7 mm. $\frac{10a}{b} = 8.5$ b M ₁₋₃ 26.7 mm.	c P ¹⁻³ 56.8 $\frac{10c}{d} = 9.42$ d P _{1-M₃} 60.1
<i>Prodissopsalis eocaenicus</i> (Matthes 1952)	a M ¹⁻³ 32 mm $\frac{10a}{b} = 8.15$	c P ¹⁻³ 81 mm. $\frac{10c}{d} = 9.76$
<i>Imperatoria gallwitzi</i> (Matthes 1952)	b M ₁₋₃ 38 mm.	d P _{1-M₃} 83 mm.

I therefore consider *Imperatoria* a *nomen nudum* and all material previously referred to it to be synonymous with *Prodissopsalis eocaenicus*.

Genus *ANASINOPA* nov.

DIAGNOSIS. Proviverrine with dental formula $\frac{3.1.24.3}{3.1.4.3}$; Skull elongate and jaws slender: P₁ two-rooted; lower premolars compressed, crowded posteriorly, length slightly greater than height; P₄ with a distinct talonid; P⁴ tubercular, parastyle smaller than metacone: M¹⁺² tritubercular, triangular, metacone and paracone close together but not connate, metastyle shearing, metaconule and paraconule present; protocone V-chaped; M³ transverse; M₁₋₃ tuberculo-sectorial, metaconid present, M₃ largest and M₁ smallest, protoconid and paraconid subequal, their height approximately equal to trigonid length, metaconid much smaller, talonid basined; M₁₊₂ talonid length slightly less than trigonid, M₃ talonid much reduced.

TYPE SPECIES. *Anasinopa leakeyi* sp. nov. The only species.

Anasinopa leakeyi gen. et sp. nov.

(Pl. 1, figs. 6, 7; Pl. 2; Text-figs. 19-22)

DIAGNOSIS. The generic characters form the basis of the diagnosis. Species about the size of the European wolf (*Canis lupus*). C₁ - M₃ = 92 mm; P₁ - M₃ = 84 mm; M₁ - M₃ = 41 mm; M¹ - M³ est. = 34 mm.

HOLOTYPE. Five pieces comprising maxillae and mandibles of one individual.

- M.19081 a Left maxilla with P⁴, M¹ and alveoli of P²⁺³.
 „ b Right „ „ M¹⁺² and alveolus of M³.
 „ c Right mandible with C, P₁₋₄, M₁₋₃.
 „ d Left „ „ M₂₊₃.
 „ e „ „ „ C and P₄.

LOCALITY. Rusinga Island, Lake Victoria, Kenya.

ADDITIONAL MATERIAL.

From Rusinga Island, Site 106:—

CMF.4044 Right M²

CMF.4045 Right M₁

From Rusinga Island, unsited:—

CMF.4018 Right mandible fragment with M₁₋₃

CMF.4019 Right M²

CMF.4020 Right M¹

CMF.4047 Left P⁴

CMF.4048 Right M²

CMF.4049 Left M₁ (trigonid only)

CMF.4050 Left P₄

CMF.4051 Left M₃ (trigonid only)

CMF.4052 Left P₂

CMF.4054 Right M₃

CMF.4055 Right mandible fragment with P₂₋₄

CMF.4056 Right M₃ (trigonid only)

CMF.4058 Left M² (broken)

From Karungu:—

CMF.4046 Left P⁴

From Maboko Island:—

CMF.4043 Left M₂

From Mfwanganu Island:—

CMF.4053 Right mandible fragment with C, P₁ roots, P₂ and part of P₃

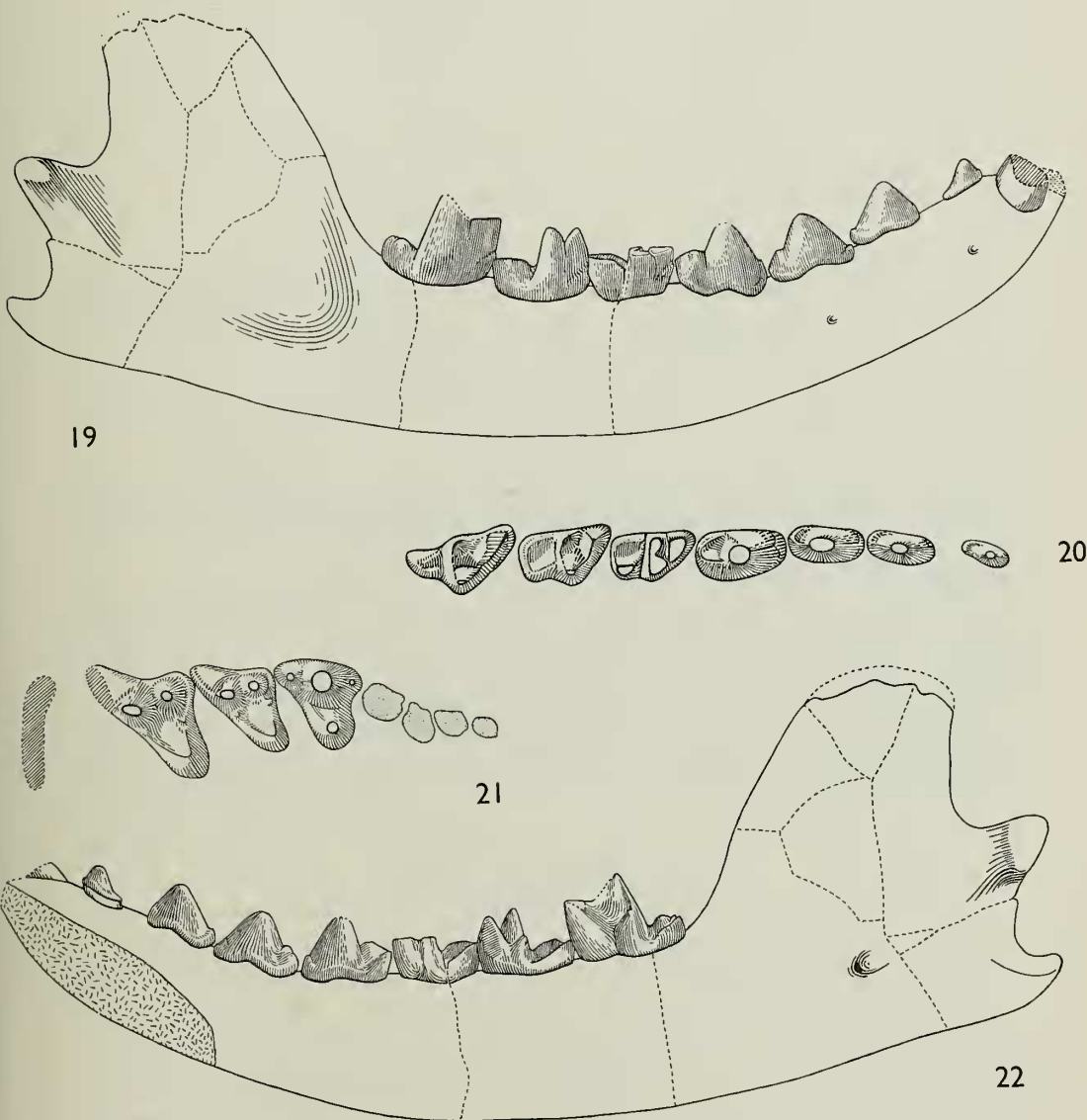
CMF.4057 Right M₂

Site unknown:—

CMF.4059 Right P₃

DESCRIPTION. None of the skull is preserved beyond that surrounding the teeth. The alveoli of the two-rooted P² and P³ are preserved and the infra-orbital foramen is present above the posterior alveolus of P³. P⁴ is tubercular; the transverse width is approximately equal to the antero-posterior length; paracone is conical with small parastyle anteriorly and metacone posteriorly; protocone well developed and slightly anterior to paracone, its posterior border continuous with metacone base, and anterior border constricted and separate from parastyle; order of cusp size commencing with the largest is paracone—protocone—metacone—parastyle; deep valley between paracone and protocone; metacone more or less connate with paracone. M¹ tuberculo-sectorial; transverse width slightly greater than antero-posterior length; paracone and metacone tubercular, metacone slightly larger than paracone, both cones close together but not fully connate; small parastyle; metastyle trenchant, connate with metacone and with weak oblique shear; external cingulum; large lunate protocone with small paraconule and metaconule on the arms. M² structurally similar to M¹ but slightly larger and metastyle more sectorial. M³ unknown; small transverse two-rooted tooth.

None of the lower incisors is preserved, but the narrow symphyseal region indicates three closely packed teeth. Only the base of the lower canine is preserved and this indicates a slender and moderate sized tooth. P_1 follows immediately



FIGS. 19-22. *Anasinopa leakeyi* gen. et sp. nov. (19) Reconstruction of right maxilla with P^4 , M^1 ²; based on M.19081a,b; occlusal aspect. (20) Right mandible with C, P_1 - P_4 , M_1 - M_3 ; occlusal aspect. (M.19081c). (21) same as Fig. 20; lateral aspect. (22) same as Fig. 20, medial aspect. Holotype (M.19081), Rusinga Is. $\times 1$.

behind the canine without any diastema; it is a small two-rooted tooth with a posterior cingulum. P_2 is much larger and P_3 is slightly larger again, with a posterior cusplet. P_4 is the largest premolar; to the main cusp is joined posteriorly a short talonid with high external cusp and low internal ridge. M_1 trigonid with metaconid considerably smaller than subequal paraconid and protoconid, the latter two cusps apparently sectorial with weak oblique shear, but trigonid cusps worn to stumps; talonid slightly shorter than trigonid, shallow basin with high buccal and low lingual bordering ridges. M_2 structurally similar to M_1 , but rather larger. M_3 with trigonid much larger than M_2 ; metaconid small, paraconid and protoconid with strongly developed oblique shear; talonid very small, less than half length of trigonid, with buccal bordering ridge and also an oblique ridge crossing inwardly over the sloping basin.

The mandible is long and slender. The symphysis is three times as long as it is high, extending as far back as P_3 . The condyle is rounded and elongated transversely; the slender curved angular process for the masseter reaches back to the level of the condyle. The coronoid with marked anterior ridge arises immediately behind M_3 and sweeps high above the condyle in a typically carnivore fashion. The anterior mental foramen is below a point between P_1 and P_2 ; the posterior foramen is below P_3 .

REMARKS. It is regrettable that so many of the genera in the sub-family are poorly known, often only from fragments. The presence of metaconids on the lower molars however distinguishes them from the hyaenodontines.

Proviverra is a very small form with connate paracone and metacone on the upper molars; premolars are short and high, and lower molars have high metaconid almost equalling protoconid. In *Paracynohyaenodon* the paraconid is very low, smaller than the metaconid. *Ischnognathus* is known only from a fragmentary mandibular symphysis and its relationship to the proviverrines must remain in doubt. *Metasinopa* is very small, lacks P_1 and has very reduced metaconids on lower molars. In *Disopsalis* the parastyle is lacking on P^4 and vestigial on the upper molars; metaconule and paraconule are not present on M^{1+2} . The diagnosis of *Geiselotherium* given by Matthes (1952) comprises nine negative statements about the genus, making it almost impossible to recognize: size alone excludes it from consideration with *Anasinopa leakyi*. Other characters could be listed which differentiate these genera from *Anasinopa*, but those given are sufficient to establish the distinction.

On the basis of molar tooth structures, the closest similarities to *Anasinopa* are to be found in *Sinopa* and *Tritemnodon*. *Tritemnodon* lacks a parastyle on P^4 ; the upper molars have connate paracone and metacone, and lack paraconule and metaconule. *Sinopa* species have large parastyle on P^4 , larger than in *Anasinopa*; M^{1+2} have widely separate paracone and metacone; in the lower dentition P_1 is single-rooted; P_4 shows little or no development of talonid; M_3 tends to be smaller than M_2 and the talonid little reduced; the talonids of M_{1-3} are more fully basined than in *Anasinopa*.

Anasinopa appears to represent a stage of evolution between *Sinopa* and *Tritemnodon* (Middle Eocene of N. America). It is less advanced than *Metasinopa* (Lower

Oligocene of Egypt) which has lost P_1 and has very reduced metaconids on lower molars.

TABLE 2

Measurements (in mm.) on holotype of *Anasinopa leakeyi* (M.19081 a-e)

					P ⁴	M ¹	M ²	M ³	
M.19081 a	a-p				13.3	12.4			
	trs				13.3	13.6			
M.19081 b	a-p					12.2	14.2		
	trs					13.0	15.3		
		C	P ₁	P ₂	P ₃	P ₄	M ₁	M ₂	M ₃
M.19081 c	a-p	8.3	6.0	9.7	11.6	13.0	12.3	14.1	16.6
	trs	5.8	3.5	5.1	5.8	6.9	7.1	8.2	8.5
M.19081 d, e	a-p	8.1				13.2		14.5	15.5
	trs	5.6				7.3		7.9	8.7

Genus *METASINOPA* Osborn 1909

DIAGNOSIS. ' P_3 , M_3 . As in *Pterodon* and *Apterodon* a basal talonid is preserved, which distinguishes this animal from *Hyaenodon*. A persistent metaconid on M_2 and M_3 distinguishes this animal from *Pterodon* and *Apterodon* and relates it to *Sinopa* and *Tritemnodon*. The lower premolars are small and P_1 absent. Heels of the lower molars small, trenchant.' [after Osborn 1909].

TYPE SPECIES. *Metasinopa fraasi* Osborn. Nearly complete left mandible (Amer. Mus. No. 14453) from the Lower Oligocene of Fayûm, Egypt.

REMARKS. Osborn (1909) established the genus on the mandible and tentatively referred to the same genus a maxilla from the same beds (Amer. Mus. No. 14452). Osborn further suggested that *Sinopa ethiopica* Andrews (1906) was probably a species of *Metasinopa*. The holotype of *S. ethiopica* is a left mandible with P_4 , M_{1-3} and Andrews provisionally placed it in *Sinopa*: Osborn's suggested reference to *Metasinopa* seems reasonable.

Metasinopa napaki sp. nov.

(Text-figs. 23, 24)

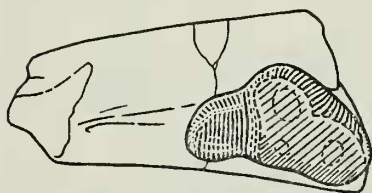
DIAGNOSIS. M_3 with talonid half as long as trigonid; metaconid present, protoconid and paraconid trenchant, talonid sloping downward and lingually from buccal ridge.

HOLOTYPE. M.19097. Left mandible fragment with broken M_3 .

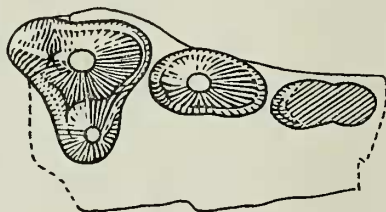
LOCALITY. Napak I, Karamoja, N.E. Uganda.

DESCRIPTION. Only a broken left M_3 is known. The protoconid and paraconid are well developed and have trenchant outer face: only the base of the metaconid is present and it appears to be a small cusp: the talonid is half as long as the trigonid and much narrower; the incipient basin has high outer and low inner margin.

REMARKS. The fragmentary evidence does not warrant any firm deductions. The specimen is provisionally included in *Metasinopa* largely for convenience and because there is no evidence for separation. To the same species is also provisionally referred a maxillary fragment with P^{3+4} (M.19096). The specimen possesses the root of P^2 and complete single cusped P^3 ; P^4 has strong protocone but no parastyle; the metacone is smaller than protocone; a cingulum is present anteriorly and buccally. The absence of a parastyle on P^4 prevents its inclusion with *Sinopa*, *Anasinopa*, *Dissopsalis* or *Prodissoptalis*. The animal was the same size as the holotype of *M. napaki*.



23



24

FIGS. 23, 24. *Metasinopa napaki* sp. nov. (23) Left mandible with M_3 . Holotype (M. 19097), Napak. (24) Maxilla with P^{3+4} . (M. 19096), Napak. $\times 2$.

Metasinopa napaki is smaller than *M. fraasi* and larger than *M. ethiopica*, and differs from both in having a proportionately longer talonid on M_3 . Until more material is available it would be best to retain *Metasinopa* for the inclusion of the following specimens:—

<i>Metasinopa fraasi</i> (type species)	Amer. Mus. 14453	Left mandible Lower Oligocene of Fayûm, Egypt.
<i>Metasinopa</i> (?) sp.	Amer. Mus. 14452	Left maxilla Lower Oligocene of Fayûm, Egypt.
<i>Metasinopa ethiopica</i>	Geol. Mus. Cairo C.10193	Left mandible Lower Oligocene of Birket-el-Qurun, Egypt.
<i>Metasinopa napaki</i>	M.19097	Left mandible Napak I, Karamoja, Uganda.
„ „	M.19096	Right maxilla Napak I, Karamoja, Uganda.

Measurements in mm. on *Metasinopa napaki*

		M ₃	P ³	P ⁴
M.19097	ant-post	12.0		
	lat	6.6		
	trigonid length	7.9		
M.19096	ant-post		8.6	9.8
	lat		5.0	9.8

Genus *DISSOPSALIS* Pilgrim 1910

DIAGNOSIS. Dental formula I ?, C_I¹, P ⁴/₄, M ³/₃: carnassials M₁¹/₂ and M₂²/₃: protocone prominent, especially on P⁴, and placed anterior to and remote from paracone: parastyle reduced: metastyle prolonged into shear: premolars robust with well developed cingulum: P⁴ almost as large as M¹; P₄ larger than M₁. Molars trenchant; M¹⁺² with large protocone, connate paracone and metacone, shearing metastyle; M³ very small: M₁ three cusped trigonid and basined talonid; M₃ paraconid-protoconid shear strong, without metaconid, talonid reduced to small peg. [After Colbert 1933].

TYPE SPECIES. *Dissopsalis carnifex* Pilgrim. The generic name reflects the double carnassial shear on two sets of molars, M₁¹/₂ and M₂²/₃.

LOCALITY AND HORIZON. Type species from Chinji, Salt Range, Siwalik Hills, India; Chinji stage, ?Middle Miocene.

In addition to the type species Pilgrim (1910, 1914) described a second and smaller species, *D. ruber*, from the same horizon and locality.

REMARKS. Pilgrim's descriptions, based on fragmentary material, are a remarkable example of his insight. Colbert (1933) had available a skull of *D. carnifex* collected on the American Museum Expedition, and has given a full account of it, together with a referred mandibular fragment.

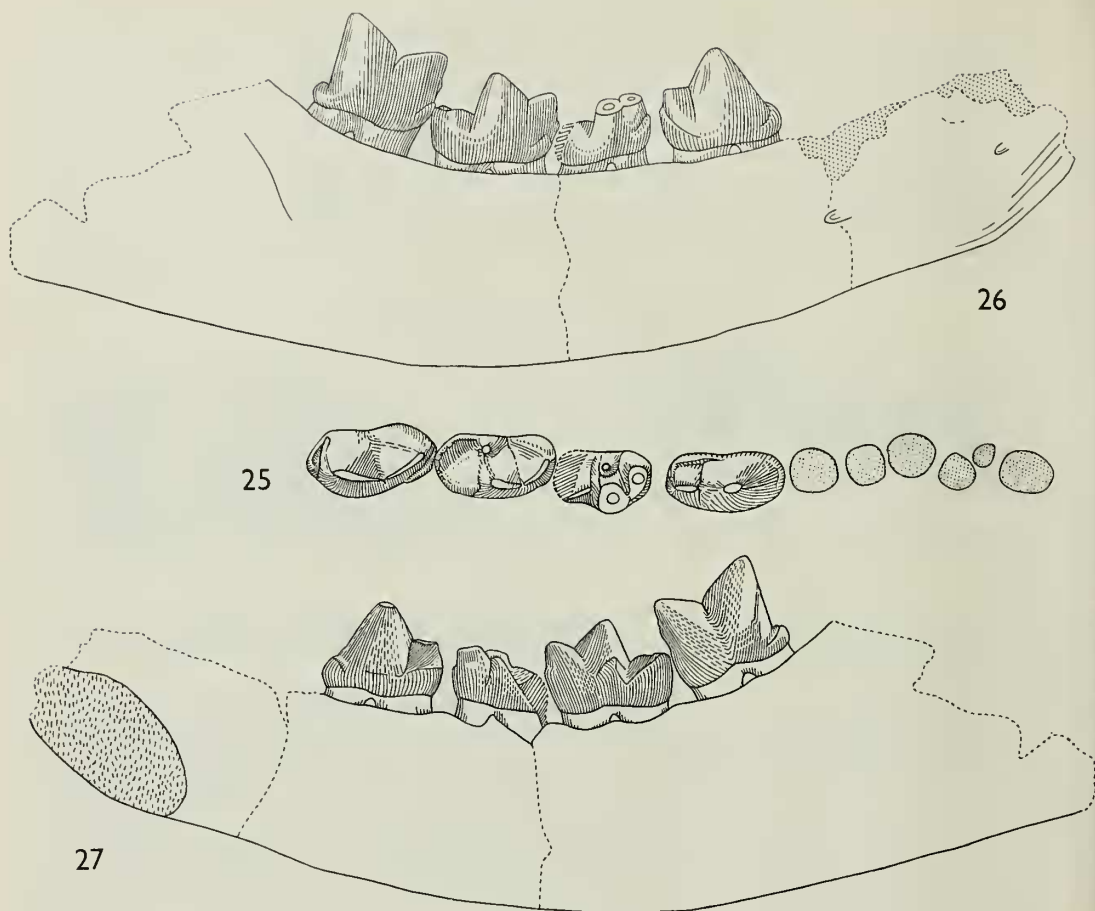
Dissopsalis pyroclasticus sp. nov.

(Pl. 3; Text-figs. 25-27)

DIAGNOSIS. Species much larger than *D. ruber* and approximately same size as *D. carnifex* but jaw shorter and teeth crowded. No diastema between premolars nor between P₁ and canine. Metaconid progressively reduced; small on M₁, vestigial on M₂ and only pin-point on M₃. Shear progressively improved from M₁ to M₃. Talonid basined on M₁₊₂; minute peg on M₃.

HOLOTYPE. M.19082. Right mandibular ramus containing P₄, M₁₋₃ and alveoli of canine, P₁₋₃. No other specimens can be assigned to the genus with certainty.

LOCALITY. Kaboor, Northern Frontier District, Kenya.



FIGS. 25-27. *Dissopsalis pyroclasticus* sp. nov. Right mandible with P_4 , M_1-3 . (25) Occlusal aspect. (26) Lateral aspect. (27) Medial aspect. Holotype (M.19082), Kaboor. $\times 1$.

DESCRIPTION. The mandible is robust and heavy. The symphyseal junction extends back as far as the middle of P_2 . The canine alveolus is not fully preserved but suggests a normal sized canine. P_1 is single rooted and crowded behind the canine. P_2 and P_3 both had large double roots and were tightly packed against each other close behind P_1 . P_4 is a large heavy tooth; the cusp is keeled anteriorly and posteriorly, the posterior keel continuing into a small accessory cusp, trenchant buccally and sloping down to a cingulum on the lingual side. M_1 is smaller than P_4 ; the trigonid is greatly worn, and of the three cusps the protoconid was larger than the paraconid, while the metaconid was very much smaller than either of the others; the talonid is broken, but must have been about the same length as the trigonid, basined with high buccal rim and low lingual rim. M_2 is larger than M_1 but structurally similar; the metaconid is reduced to a minute peg and the paraconid-protoconid

has a strong oblique shear. M_3 has a larger trigonid than M_2 and hence bigger shear area on paraconid-protoconid; the metaconid is detectable only as a pin-head projection of enamel on the postero-internal slope of the protoconid; the talonid is reduced to a small peg.

REMARKS. The similarity of the new species to *D. carnifex* is striking. The differences are so small that it is difficult to determine which is the more or less advanced. The shorter jaw and more crowded dentition, together with the more reduced talonid on M_3 suggest that *D. pyroclasticus* is slightly more advanced than *D. carnifex*. The robust jaw and heavy premolars are reminiscent of *Quercytherium* from the Phosphorites du Quercy, though in this genus the molars are less specialised.

Measurements (in mm.) on holotype of

Dissopsalis pyroclasticus (M.19082)

	P_4	M_1	M_2	M_3
a-p	16.0	ca. 13.0	17.5	16.5
trs	9.0	7.8	8.7	9.0

Subfamily **HYAENODONTINAE** Trouessart

DIAGNOSIS. Hyaenodontidae with narrow skull and long face; M_3^3 or M_3^2 ; molars sectorial, length greater than width; M^3 small and transverse or absent; M^{1+2} with paracone and metacone completely or nearly connate, protocone reduced or absent; lower molars without metaconid, talonid vestigial or absent.

REMARKS. Simpson (1945) listed seven genera in the subfamily; of these, four are clearly good genera, *Pterodon*, *Apterodon*, *Metapterodon*, and *Hyaenodon*: *Propterodon* is less well known. *Hemipsalodon* is a synonym of *Pterodon* and *Dasyurodon* a synonym of *Apterodon*. To these is here added a new genus, *Leakitherium*.

TABLE 3
Distribution of Hyaenodontine Genera

	EUROPE	AFRICA	ASIA	N. AMERICA
LOWER MIOCENE		<i>Hyaenodon</i>		
UPPER OLIGOCENE	<i>Hyaenodon</i>			
MIDDLE OLIGOCENE	<i>Hyaenodon</i> <i>Apterodon</i>		<i>Hyaenodon</i>	<i>Hyaenodon</i>
LOWER OLIGOCENE	<i>Hyaenodon</i> <i>Apterodon</i> <i>Pterodon</i>	<i>Hyaenodon</i> <i>Apterodon</i> <i>Pterodon</i> <i>Metapterodon</i> <i>Leakitherium</i>	<i>Hyaenodon</i>	<i>Hyaenodon</i> <i>Pterodon</i>
UPPER EOCENE	<i>Hyaenodon</i> <i>Pterodon</i>		<i>Hyaenodon</i> <i>Pterodon</i> <i>Propterodon</i>	<i>Hyaenodon</i> <i>Pterodon</i>
MIDDLE EOCENE	<i>Propterodon</i>			

Genus *METAPTERODON* Stromer 1926

DIAGNOSIS. Hyaenodontine with M^3_3 ; P^3 – M^3 slowly increase in size; M^3 small and transverse; M^{1+2} sectorial with buccal cingulum, parastyle minute or absent, protocone present; P^3 simple two rooted.

TYPE SPECIES. *M. kaiseri* Stromer from Elizabethfeldern, S.W. Africa; horizon stated by Stromer (1926) to be Lower Miocene.

A second species from Rusinga is described below. *Pterodon biincisivus* Filhol (1876) from the Lower Oligocene of Phosphorites du Quercy, France is here transferred to the genus *Metapterodon*.

REMARKS. Stromer's original diagnosis placed much emphasis on skull features, in particular the position of the infra-orbital foramen. I consider these plastic architectural modifications and thus variable from species to species, depending largely on size and adaptation requirements. From Schlosser's remarks, it appears that he compared *Metapterodon kaiseri* with only two species of *Pterodon*, the type species *P. dasyuroides* and *P. africanus* from the Fayûm. He makes no mention of the other five species of *Pterodon* described prior to 1926.

A critical phrase in Stromer's diagnosis is "Zahngrösse von P^3 bis M^2 stark zunehmend". With this I disagree; the tooth size, as seen in Table 4 does increase from P^3 to M^2 , but not greatly. M^2 is only about one-third as long again as P^4 . The determinative feature is that the increase is much less than that found in *Pterodon* species. In *Metapterodon* the reduced parastyle and well developed protocone (as noted by Stromer) form clear generic distinctions from *Pterodon*.

On the basis of the above diagnosis *Pterodon biincisivus* Filhol falls within the genus *Metapterodon*; it also has the infra-orbital foramen above the border of P^3 and P^4 as in *M. kaiseri*.

Metapterodon kaiseri Stromer

(Pl. 4, fig. 1; Text-fig. 28)

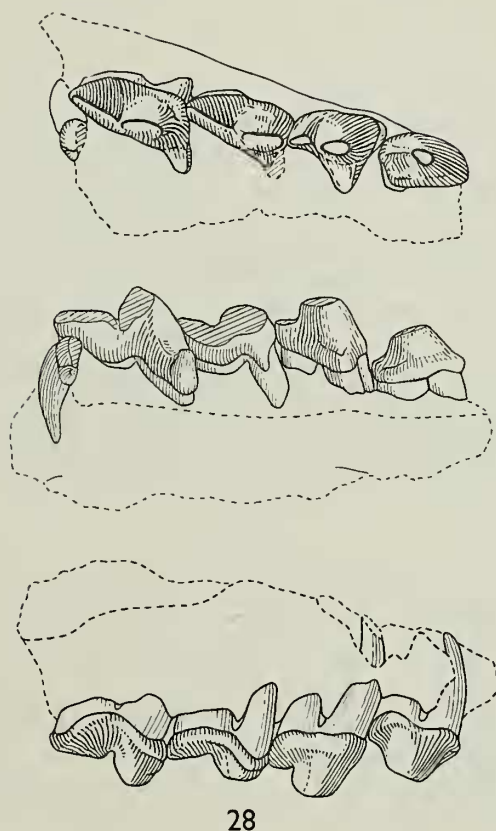
1926 *Metapterodon kaiseri* Stromer: 110–112, pl. 40, figs. 13, 14

DIAGNOSIS. *Metapterodon* species of about size of *Alopex*: skull elongate and slender, infra-orbital foramen above border of P^3 – P^4 , P^3 simple two-rooted: upper molars with outer cingulum, parastyle absent from P^4 and M^1 , rudimentary on M^2 ; protocone well developed on M^{1+2} . [After Stromer 1926].

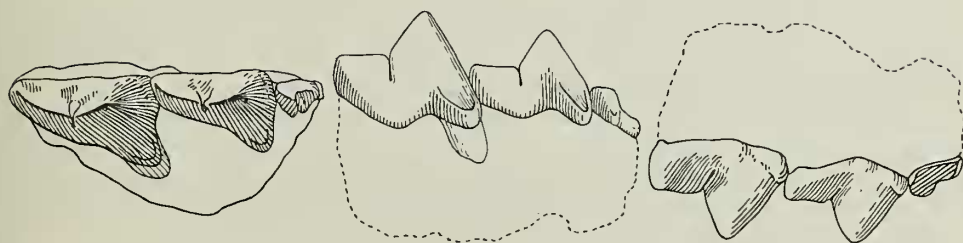
HOLOTYPE. Left skull fragment with P^3 – M^2 , from Elizabethfeldern, S.W. Africa. Stromer (1926) considered the deposit to be Lower Miocene in age on the basis of similarity of fauna with East African fauna. 1926 \times 1 Munich.

ADDITIONAL MATERIAL: CMF.4038. Right maxilla with P^3 – M^3 from Karungu, Kavirondo Gulf, Kenya. CMF.4066a Left maxillary fragment with P^4 – M^2 , teeth broken. CMF.4066b Right mandibular symphysis with broken canine root and two broken premolars. CMF.4066c Left mandibular fragment with roots of molars. All from Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION: On specimen CMF.4038 little more than the bone around the teeth is preserved. Posteriorly the root of the jugal arch is preserved: this rises nearly



28



29

FIGS. 28, 29. *Metapterodon kaiseri* Stromer and *Metapterodon zadoki* sp. nov. (28) *M. kaiseri*. Right maxilla with P^3 - M^3 ; occlusal, medial and lateral aspects. (CMF.4038), Karungu. (29) *M. zadoki*. Right maxilla with M^1 2 ; occlusal, medial and lateral aspects. Holotype (M.19094), Rusinga Is. Both 1.5.

vertically and shows no tendency to spread horizontally. The infra-orbital canal issues to the bone surface in the space between the root tips of P^3 and P^4 . P^3 is a simple two-rooted tooth with prominent internal cingulum and small posterior accessory cusp. P^4 is three rooted, larger than P^3 , with robust central cusp, well developed posterior accessory cusp and protocone of about same size; the protocone is centrally placed opposite the main cusp and the external cingulum is well marked. M^1 is slightly larger than P^4 ; the protocone is missing, but from the root it appears to have been about as large as that on P^4 ; the paracone and shearing metacone are about equal in length though in the holotype both are much worn. The external cingulum is prominent and continues anteriorly round the paracone. M^2 is larger than M^1 , with prominent protocone placed well anteriorly and remote from the paracone, which is a stout conical cusp from whose anterior border arises a minute parastyle; the metacone is about the same length as the paracone and forms a strong shearing blade, separated by a cleft from the paracone; the angle of shear is very low, being almost parallel to the longitudinal axis; as in M^1 the external cingulum fold continues anteriorly around the paracone. M^3 is a small peg-like transverse tooth, with a single transversely flattened root: the crown is worn but enough remains to discern the presence of a protocone and larger paracone, beyond which probably lay a small parastyle.

The crowns of P^{3+4} and the paracone of M^1 are worn flat and the shearing metacones of M^{1+2} show evidence of much wear: neither the protocone on P^4 nor M^2 shows any wear, suggesting a deep or very reduced talonids on the lower molars.

REMARKS. The strongly sectorial M^{1+2} , together with the prominent protocone suggest a degree of evolution comparable with *Pterodon*. The genus has not the advanced specialization of *Hyaenodon*, nor the more tubercular features of *Apterodon*. A picture emerges of *Metapterodon* species as medium sized hunters comparable with foxes, as opposed to the heavier built and larger *Pterodon* species, more comparable to the hyaenas.

There are no features on which the S.W. African and Rusinga specimens can be seen to differ. The table of measurements for both specimens shows the close similarity in size: (the figures for the S.W. African specimen are taken from Stromer (1926): in this the M^3 is missing and the P^3 is rather narrower).

On specimen CMF.4066a all three teeth are broken (P^4 - M^2), but enough of M^2 is preserved to make identification certain. The only difference from the specimen described above is a slightly greater size; this however is small and not considered to be of taxonomic importance in view of the proximity of Karungu and Rusinga, and the general resemblance of their mammal faunas.

***Metapterodon zadoki* sp. nov.**

(Pl. 4, fig. 2; Text-fig. 29)

DIAGNOSIS. Slightly larger than the type species; upper molars robust with strong shear, parastyle absent from M^{1+2} , protocone very reduced on M^{1+2} .

The specific name pays tribute to Zadok, the keen-eyed Luo collector on Rusinga.

HOLOTYPE. M.19094. Right maxillary fragment with M^{1+2} . Rusinga Island, Lake Victoria, Kenya.

DESCRIPTION. The holotype is the only known specimen of the species. None of the maxilla save that which supports the teeth is preserved. A posterior fragment of P^4 is present. M^1 has a high conical paracone and trenchant metacone, both of about equal width; the shear of the metacone is continued onto the paracone, thus providing a large shearing surface: there is no parastyle, but a prominent external cingulum wraps round the anterior margin of the tooth: the vestigial protocone is little more than a low enamel-capped root placed far anteriorly, clear of the extended shearing metacone-paracone. M^2 is an enlarged edition of M^1 , with which it corresponds in all details.

REMARKS. The most notable differences between *M. zadoki* and *M. kaiseri* relate to the carnassial specialization. *M. zadoki* is the more advanced, having a shear extending onto the paracone, reduced protocone and being without parastyle: this is a stage of development which could easily be derived from *M. kaiseri*.

TABLE 4
Measurements of *Metapterodon* species (in mm.)

		<i>Metapterodon kaiseri</i> Stromer 1926 S.W. Africa Holotype	<i>Metapterodon kaiseri</i> CMF.4038 Kenya	<i>Metapterodon kaiseri</i> CMF.4066a Kenya	<i>Metapterodon zadoki</i> M.19094 Kenya Holotype	<i>Metapterodon biincisivus</i> Filhol 1876 Phosphorites du Quercy Holotype
P^3	a-p	8	7.8	—	—	12.0
	trs	3	4.9	—	—	5.4
P^4	a-p	7.5	8.6	9.0.	—	11.0
	trs	6.5	7.4	8.2	—	
M^1	a-p	9	9.4	9.4.	10.9	15.0
	trs	7	8.5.	8.7.	7.3	11.7
M^2	a-p	10.5	10.6	12.3	12.2	16.2
	trs	10.5	8.5	9.3	8.7	14.6
M^3	a-p	? 2	2.8	—	—	4.8
	trs	? 3	6.4	—	—	12.0

*approximate

Genus *PTERODON* de Blainville 1839

DIAGNOSIS. Hyænodontine with M_3^3 ; P^3 - M^2 rapid increase in size; premolars short and high; M^{1+2} with small protocone, parastyle large; lower molars with strong paraconids, talonids reduced; molars strongly trenchant: infra-orbital foramen above P^3 .

TYPE SPECIES. *Pterodon dasyuroides* de Blainville from the Lower Oligocene of the Phosphorites du Quercy, France. Also recorded from the same horizon in several parts of France, Germany and the Isle of Wight.

The following species have also been described:—

P. grandis (Cope 1885). Lower Oligocene, White River Beds, Saskatchewan, Canada.

P. magnus Rutimeyer (1891). Middle Eocene, Switzerland.

P. africanus Andrews (1903). Lower Oligocene, Fayûm, Egypt.

P. leptognathus Osborn (1909). „ „ „ „

P. phiomensis Osborn (1909). „ „ „ „

P. hyænoides Matthew & Granger (1925b). Upper Eocene, Shara Murun, Mongolia.

P. californicus Stock (1933). Upper Eocene, California.

REMARKS. All species are strikingly similar and vary mainly in size. None is plentiful or fully known. Three other species described from Europe, *P. parisiensis* de Blainville (1841), *P. cuvieri* Pomel (1847b) and *P. coquandi* Pomel (1853), are considered synonyms of *P. dasyuroides*. *P. biincisivus* Filhol (1876) is discussed above and considered to be a species of *Metapterodon*.

Pterodon africanus Andrews

(Pl. 4, fig. 3; Text-figs. 30-32)

1903 *Pterodon africanus* Andrews: 342, text-fig. 3.

DIAGNOSIS. Species distinguished from others in the genus on size; all except *P. grandis* and *P. nyanzae* are smaller. *P. grandis* is two-thirds as large again; *P. nyanzae* lacks an anterior keel on P^4 and M^1 .

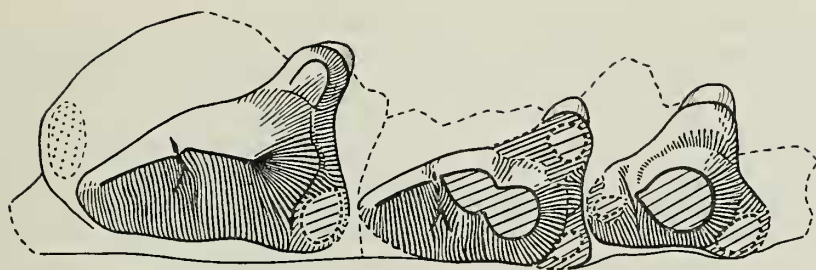
HOLOTYPE. M.8503. Right ramus of mandible with P_{2-4} , M_{1-3} from the fluvio-marine beds, Lower Oligocene, north of Birket-el-Qurun, Fayûm, Egypt (Andrews 1906: 220, pl. 19, fig. 3).

OTHER MATERIAL. In addition to the holotype there exist skulls and mandibles described by Andrews (1906) and Schlosser (1911). Further specimens from Uganda and Kenya are referred to below.

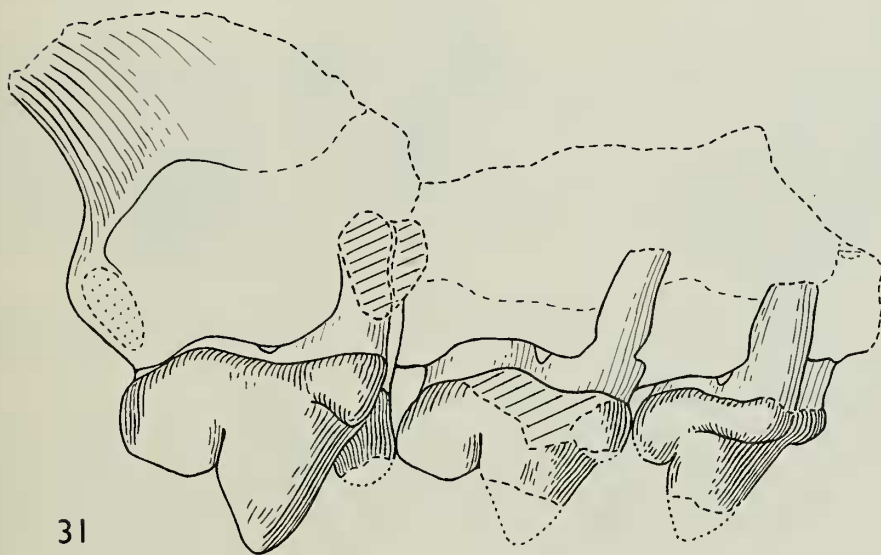
M.19090. Left maxilla with P^4 , M^{1+2} , Napak I, Karamoja, Uganda.

CMF.4024. Right P^4 , Rusinga Island, Kavirondo Gulf, Kenya.

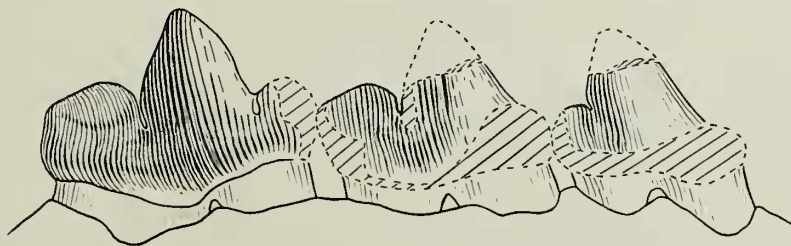
DESCRIPTION. On the new maxilla from Napak the crowns of the teeth are broken but otherwise in good condition. On P^4 the strong paracone has a posterior keel and beyond a keeled accessory cusplet; the protocone has a very heavy root,



30



31



32

FIGS. 30-32. *Pterodon africanus* Andrews. Left maxilla with P⁴, M¹⁻². (30) Occlusal aspect. (31) Medial aspect. (32) Lateral aspect. (M.19090), Napak. $\times 1$.

but is not elevated into a cusp and forms instead an internal shelf; the parastyle is broken externally and is slightly smaller than the posterior cusplet. M^1 is much larger than P^4 ; the small protocone is placed very anteriorly and its border projects beyond that of the smaller parastyle: the large paracone is characterised by the presence of a strong external groove and weak internal groove, posterior to which the cusp is trenchant internally; (the groove is indicative of the fusion of the paracone and metacone): a notch separates the paracone from the trenchant blade of the elongate metastyle. M^2 is a massive tooth with a high paracone, keeled posteriorly to meet the long trenchant metastyle; the parastyle is slightly larger than the protocone, which arises anteriorly, well removed from the paracone; the paracone-metastyle blade lies at about 20° to the longitudinal axis of the jaw. The small alveolus denotes a vestigial transverse M^3 .

REMARKS. The similarity of the East African material to the Fayûm specimens is so close and the differences so trivial, I can find no case for separating them into different species. The size of the Fayûm and Napak teeth are very similar, though few measurements in the table are precise due to damage affecting nearly all teeth. The Fayûm skull (C.10192) is rather lighter in build than the Napak maxilla, while the holotype jaw has a massiveness more akin to the new find. These differences are trivial and amount to no more than individual variations; possibly the holotype and the Napak specimen are male and the Fayûm skull female.

The external groove on the paracone-metacone of M^1 is barely noticeable on the Fayûm skull, but distinctive on the Napak maxilla: otherwise there are no distinguishing features. The Rusinga premolar tooth, CMF.4024, referred to the species is a very worn and isolated P^4 .

Considerable interest attaches to the specific linkage of East African sites with Fayûm, since the Fayûm stratigraphy is well dated and the hyaenodontids appear to be good stratigraphic indicators. This aspect is discussed at the end of the paper.

Pterodon nyanzae sp. nov.

(Text-figs. 33-35)

DIAGNOSIS. Species larger than *P. africanus* and smaller than *P. grandis*. Distinguished from *P. africanus* by presence of anterior keel on P^4 and M^1 .

Name derived from Nyanza, the province of Kenya in which the species occurs.

HOLOTYPE. M.19091. Isolated right P^4 from Ombo, Kavirondo Gulf, Kenya.

PARATYPES. In addition to the holotype, the type locality has yielded two paratype specimens M.19092 isolated left P^4 , broken and M.19093 isolated right M^1 , broken.

Another specimen CMF.4007, a very broken left P^4 from Rusinga Island, site 3, is also referred to the species. A right M^2 (UMP 64.33) is recorded from Napak II A.

DESCRIPTION. The holotype is a nearly complete right P^4 . The tooth has three roots, anterior, posterior and internal; all are heavy straight-sided roots, the internal the largest and the anterior the smallest. The tooth has a large central conical cusp, accessory cusplets and an internal shelf. The apex of the central cusp is worn flat and the thick enamel is elevated into a ridge anteriorly and posteriorly, the posterior ridge being the higher. The anterior accessory cusplet is much worn by occlusion with P_4 and the posterior cusplet is strongly keeled: the internal sloping shelf is broad and without any cusp development.



FIGS. 33-35. *Pterodon nyanzae* sp. nov. Right P^4 . (33) Occlusal aspect. (34) Medial aspect. (35) Lateral aspect. Holotype (M.19091), Ombo. $\times 1$.

The paratype M.19092 is a left P^4 and although part of the internal shelf and all the roots are missing, it is an exact mirror image of the holotype, displaying the same degree of wear. The paratype M.19093 is a right M^1 with only the anterior half preserved: the tooth is three rooted and probably the anterior root is the largest. The paracone and metacone are completely fused though there remains a distinct groove externally on the conical cusp, truncated by wear.

CMF.4007 consists only of the posterior half of the central cusp and the posterior keeled cusplet. In size and character there is nothing to distinguish it from the two P^4 teeth described above.

REMARKS. The three teeth from the same site may be from the same individual, judging from the degree of wear on the crowns. The table of measurements shows they are considerably larger than *P. africanus* teeth, much more so than would be expected by individual variation. The well marked anterior keel on both P^4 and M^1 clearly distinguishes these teeth from the *P. africanus* specimens of Fayûm and of Napak.

TABLE 5

Measurements (in mm.) for *Pterodon africanus*
and *Pterodon nyanzae*

		P ⁴	M ¹	M ²
<i>P. africanus</i>	a-p	25	29	36
C.10192	trs	20	20	23
Fayûm, Egypt				
<i>P. africanus</i>	a-p	26	32	38
M.19090	trs	22	21	29
Napak, Uganda				
<i>P. africanus</i>	a-p	25		
CMF.4024	trs	22		
Rusinga, Kenya				
<i>P. nyanzae</i>				
(Holotype.)	a-p	30		
M.19091	trs	24		
Ombo, Kenya				
<i>P. nyanzae</i>	a-p	29		
M.19092	trs	24		
Ombo, Kenya				
<i>P. nyanzae</i>	a-p		—	
M.19093	trs		28	
Ombo, Kenya				

Genus **LEAKITHERIUM** nov.

DIAGNOSIS. Hyaenodontine without M³; M¹⁺² highly sectorial, protocone greatly reduced on M²; molars with connate paracone and metacone and shearing metastyle; P⁴ with protocone and prominent parastyle, central paracone, metacone and trenchant metastyle.

TYPE SPECIES. *Leakitherium hiwegi* sp. nov.

Leakitherium hiwegi sp. nov.

(Pl. 4, figs. 4, 5; Text-figs 36, 37)

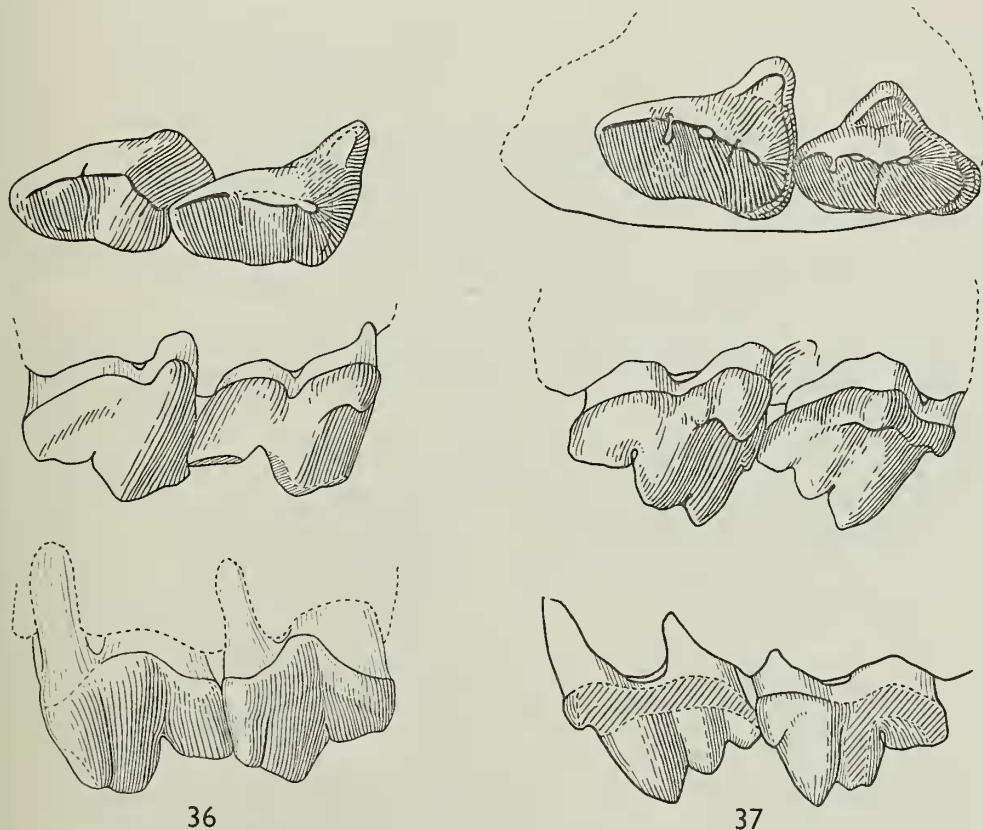
DIAGNOSIS. As for genus. Species about size of leopard.

HOLOTYPE. M.19083. Left maxillary fragment with M¹⁺² from Rusinga Island, Lake Victoria, Kenya. The only species.

PARATYPE. CMF.4025. Left maxilla with M¹ and P⁴ from Rusinga Island, site 3, Lake Victoria, Kenya. This is the only other specimen of the species.

DESCRIPTION. None of the skull other than the bone surrounding the teeth is known. The holotype has the bone preserved to the level of the orbit and the begin-

ning of the jugal is discernible. P^4 has high central cusp and prominent protocone opposite: the parastyle is smaller than the protocone: the tooth is not well preserved posteriorly but the metacone probably formed a low cusp followed posteriorly by a trenchant metastyle. M^1 is larger than P^4 : the metacone is connate with and slightly larger than the paracone; the cusps are divided buccally by a groove and are sectorial on the inner side. The protocone is placed anteriorly, level with the paracone: the parastyle is displaced buccally and much smaller than on P^4 : the trenchant metastyle continues posteriorly the shear of the metacone. M^2 is about the same size as M^1 and structurally similar, save that the protocone is very reduced and the parastyle absent.



FIGS. 36, 37. *Leakitherium kiwegi* gen. et sp. nov. (36) Left maxilla with M^1 2, occlusal, medial and lateral aspects. Holotype (M.19083), Rusinga Is. (37) Left maxilla with P^4 , M^1 , occlusal, medial and lateral aspects. (CMF.4025), Rusinga Is. $\times 1.5$.

REMARKS. The presence of two carnassial upper molars and the absence of M^3 places the species immediately in the Hyaenodontinae. Within this subfamily only *Hyaenodon* is known to lack M^3 and on *Hyaenodon* the protocones and talonids are

also lacking. *Leakitherium* displays the clear tendency to greater carnassial efficiency as seen in the morphological series *Apterodon*—*Pterodon*—*Leakitherium*—*Hyaenodon*. The strongly sectorial molars, with cutting plane directed anteroposteriorly and not transversely, are characters found elsewhere among the *Hyaenodontidae* only in *Pterodon* and *Hyaenodon*. The loss of M^3 in *Leakitherium* without loss of protocones save reduction on M^2 , implies a less advanced specialization than in *Hyaenodon*.

Measurements (in mm.) for *Leakitherium hiwegi*

	CMF.4025	M.19083		
	P ⁴	M ¹	M ¹	M ²
ant-post	? 16.4	16.0	16.5	16.0
lat	11.3	14.3	6.0	? 13.0

Genus *HYAENODON* Laizer & Parieu 1838

DIAGNOSIS. Dental formula $\frac{3.1.4.2}{3.1.4.3}$; M^2 with shallow groove on completely connate paracone and metacone; molars without protocone; metastyle strongly elongated, especially on M^2 . Main carnassial pair M^2_3 , with M^1_2 as accessory carnassials. M_3 without talonid, M_{1+2} with or without vestigial talonid.

TYPE SPECIES. *Hyaenodon leptorhynchus* Laizer & Parieu.

STRATIGRAPHIC RANGE. Upper Eocene to Upper Oligocene, Europe; Upper Eocene to Middle Oligocene, Asia and N. America; Lower Oligocene to Lower Miocene, Africa.

The following species have been attributed to the genus:—

Europe

- H. leptorhynchus* Laizer & Parieu 1838
- H. brachyrhynchus* de Blainville 1842
- H. vulpinus* Filhol 1876
- H. compressus** Filhol 1876
- H. minor* Gervais 1848-52
- H. bavaricus* Dehm 1935
- H. aimi* Cooper 1926
- H. parisiensis* Gervais 1848-52
- H. martini* Depéret 1917
- H. Cayluxi* Filhol 1876
- H. dubius** Filhol 1872
- H. requieni* Gervais 1846
- H. aymardi** Filhol 1881
- H. herberti* Filhol 1876
- H. milloquensis* Martin 1906
- H. filholi* Schlosser 1887
- H. ambiguus** Martin 1906
- H. gervaisi* Martin 1906
- H. laurillardi* Pomel 1853
- H. exiguus* Gervais 1876

*species also occur in Asia

N. America

- H. horridus* Leidy 1853
- H. cruentus* Leidy 1853
- H. crucians* Leidy 1853
- H. mustelinus* Scott 1894
- H. paucidens* Osborn & Wortman 1894
- H. montanus* Douglass 1901
- H. leptcephalus* Scott 1887
- H. vetus* Stock 1933
- H. minutus* Douglass 1901

Asia

- H. pervagus* Matthew & Granger 1924
- H. eminus* Matthew & Granger 1925a
- H. yuanchensis* Young 1937

Africa

- H. brachycephalus* Osborn 1909
- H. andrewsi* sp. nov.
- H. matthewi* sp. nov.
- H. pilgrimi* sp. nov.

REMARKS. No genus among the hyaenodonts is in so much need of revision as *Hyaenodon*. No less than 33 species are recorded in the literature and the genus has a much greater stratigraphic range than any other in the subfamily. A survey of the species makes it clear that either there is a very wide range of variation within the genus or several genera are involved, or possibly both factors operate together to produce the present chaotic assemblage of forms. The diagnoses of species within the genus rest almost entirely on size differences; morphological characters used have been found to be inconstant. Much of the known material comprises mandibular remains and in an attempt to unravel the species I plotted the distribution of the following six characters:—

- a. Presence or absence of P_1 .
- b. P_1 with 1 or 2 roots.
- c. Mental foramina below P_1 , between P_2 and P_3 , or below P_3 .
- d. Presence or absence of buttress on antero-external margin of M_3 .
- e. Presence or absence of trace of talonid on M_3 .
- f. Size relation of protoconid to paraconid.

P_1 is almost always present and usually has two roots. There is invariably a mental foramen below P_1 , frequently below P_3 and sometimes one or more either below P_2 or between P_2 and P_3 . On M_3 the buttress is highly variable, being present on some individuals and absent from others of the same species: it is more usually present than absent. Relatively few specimens show trace of a talonid on M_3 . The protoconid tends to be larger than the paraconid, sometimes by a considerable margin, and occasionally the two are almost equally long. None of these characters, either singly or in combination, can be used for specific determination. Size is a not very satisfactory criterion on which to base a diagnosis; there is probably a wide range within each species, if only this could be checked, and much overlap.

Nine North American species are described, ranging from the very large *H. horridus* to the small *H. mustelinus*. Three species are recorded from Mongolia and China and one from the Fayûm of Egypt. The remaining 20 species are European and of these 4 also occur in Asia. Many are poorly known and synonyms are inevitably rampant. The stratigraphic distribution in Europe illustrates an Upper Eocene group of species and a Middle-Upper Oligocene group. The Upper Eocene group has a possible forerunner in the Middle Eocene, *Propterodon*: this form from Egerkingen is poorly known but may be a link in the line from proviverrines to hyaenodontines.

In the absence of a full scale revision of the genus I find it best to make a compromise. The African species appear to have one important character in common which is rare if not truly absent from all others, and on this basis they are grouped into a new subgenus. When more material is available, it will probably be possible to elevate this taxon to generic rank.

Subgenus *ISOHYAENODON* nov.

DIAGNOSIS. *Hyaenodon* species in which the protoconid and paraconid of M_3 are approximately equal in length.

TYPE SPECIES. *Hyaenodon (Isohyaenodon) andrewsi* sp. nov.

In addition to the type species, the following are included in the subgenus *Isohyaenodon*: *Hyaenodon brachycephalus* Osborn, *H. matthewi* sp. nov., and *H. pilgrimi* sp. nov. The three new species, *H. andrewsi*, *H. matthewi* and *H. pilgrimi* are all smaller than *H. brachycephalus*, and *H. pilgrimi* is by far the smallest known *Hyaenodon* species.

TABLE 6

Distribution of *Hyaenodon* species

	EUROPE	AFRICA	ASIA	N. AMERICA
LOWER MIOCENE		<i>andrewsi</i> <i>matthewi</i> <i>pilgrimi</i>		
UPPER OLIGOCENE	<i>milloquensis</i> <i>bavaricus</i> <i>leptorhynchus</i> <i>gervaisi</i>			
MIDDLE OLIGOCENE	<i>leptorhynchus</i> <i>gervaisi</i> <i>brachyrhynchus</i> <i>vulpinus</i> <i>laurillardii</i> <i>exiguus</i> <i>compressus</i> <i>martini</i> <i>cayluxi</i> <i>dubius</i> <i>ambiguus</i> <i>filholi</i>		<i>pervagus</i> <i>aymardi</i> <i>ambiguus</i> <i>compressus</i> <i>dubius</i>	<i>mustelinus</i> <i>paucidens</i> <i>leptocephalus</i> <i>horridus</i> <i>cruentus</i> <i>crucians</i>
LOWER OLIGOCENE	<i>aymardi</i>	<i>brachycephalus</i> <i>andrewsi</i>	<i>yuanchensis</i>	<i>horridus</i> <i>cruentus</i> <i>crucians</i> <i>montanus</i> <i>minutus</i>
UPPER EOCENE	<i>aimi</i> <i>minor</i> <i>parisiensis</i> <i>requieni</i> <i>herberti</i>		<i>eminus</i>	<i>vetus</i>

Hyænodon (Isohyænodon) andrewsi sp. nov.

(Pl. 4, fig. 6; Text-figs. 38-40)

DIAGNOSIS. *Isohyænodon* of about the same size as *H. minor*. M_3 with vestigial talonid.

The trivial name is a tribute to C. W. Andrews (1866-1924), a profound student of fossil mammals who made a singular contribution to our knowledge of the Fayûm faunae.

HOLOTYPE. M.15048. Right mandibular fragment with M_{1-3} . From Ombo, Kavirondo Gulf, Kenya.

ADDITIONAL MATERIAL. In addition to the holotype the following are referred to the species:

CMF.4021 Right mandible with P_{3+4} , M_{2+3} , alveoli of C, P_{1+2} , M_1 . Moruorot South, Northern Frontier District, Kenya.

CMF.4022 Right mandibular fragment with M_3 and alveoli of M_{1+2} . Songhor, Kavirondo Gulf, Kenya.

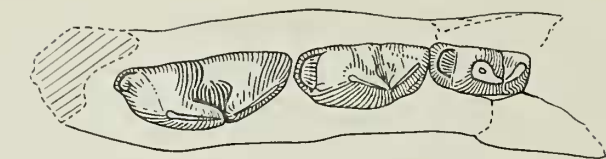
CMF.4023 Broken left M_3 . Rusinga Island, site 3, Kavirondo Gulf, Kenya.

C.8812-13 Fragment of right mandible with M_3 ; from Fluvio-marine beds, Birket-el-Qurun, Fayûm, Egypt.

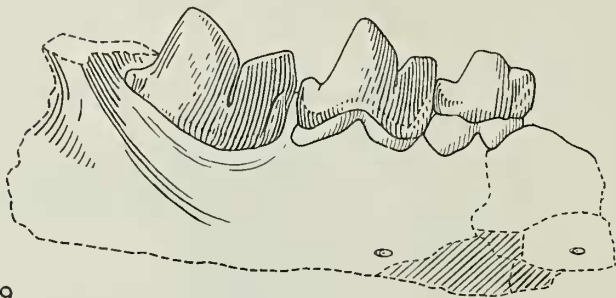
DESCRIPTION. The holotype is much broken and little of the mandible remains other than that part enclosing the tooth roots, but the surviving parts give the impression of robustness.

M_1 is small and much worn, in contrast to all other teeth which are unworn, M_3 being not even fully erupted. On M_1 the protoconid is rather larger than the paraconid: the summit of the protoconid is truncated by wear and the paraconid appears to have been damaged during life since on the broken anterior surface the fracture edges are not fresh; these two cusps are separated by a shallow cleft, and the trenchant labial face is longitudinally aligned: the small low talonid slopes antero-medially. M_2 is much larger than M_1 ; the paraconid and protoconid form good shearing facets; the talonid is proportionately smaller than on M_1 and a small buttress is present near the base of the antero-labial edge of the paraconid. The large M_3 is almost fully erupted and completely unworn; the paraconid is as broad as but not as high as the protoconid and the cleft which separates them extends almost to the base of the tooth; the carnassial shear is only slightly oblique and a small buttress is again present on the outer edge of the paraconid: a vestigial talonid is present on the postero-internal border.

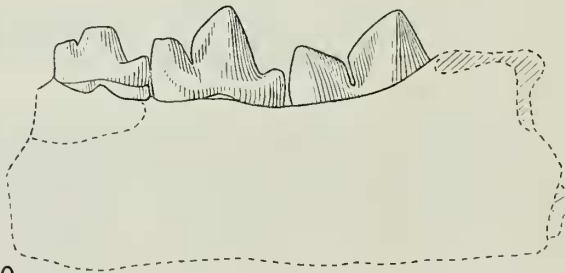
An anterior mandibular fragment with three premolars has been glued to the holotype described, although its true association with this is dubious. There is very little actual bone contact and this does not form a neat join. I suspect that at best this is an anterior fragment with a middle section between the two parts missing, or else it has nothing to do with *H. (I.) andrewsi*. This second fragment, if it truly



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39



40

FIGS. 38-40. *Hyaenodon (Isohyaenodon) andrewsi* sp. nov. Right mandible with M_{1-3} . (38) Occlusal aspect. (39) Lateral aspect. (40) Medial aspect. Holotype (M.15048), Ombo. $\times 1.5$.

belongs to the same individual, may represent three milk premolars and part of the alveolus of the canine; the premolars are small in comparison with the molars of the holotype. The first is a small two-rooted tooth with posterior accessory cusp lying very close behind the canine. The second is similar but slightly larger. The third premolar is more robust with high pointed central cusp and low posterior cusp; a cingulum is present anteriorly and postero-internally. The first two premolars appear to belong to the same dentition; compared with the permanent molars, their small size suggests milk teeth; their position with respect to the canine makes it likely that they are DP_{1+2} , though it is possible they could be DP_{2+3} , allowing for a very small first milk premolar, or even its absence.

The second mandible, from Moruorot, is less broken but fewer teeth are present. The jaw is long, shallow and strongly built; anteriorly there is a long symphysis and posteriorly the mandibular foramen issues well behind M_3 . Mental foramina are present under P_1 and P_3 . The angular process of the jaw is stout and dorso-ventrally flattened; the masseteric fossa deep. The posterior part of the canine alveolus is large and ovoid in section. P_1 and P_2 are absent: P_1 was small and apparently single rooted, and P_2 much larger and two-rooted, the posterior root being preserved in the alveolus. The crown of P_3 is much worn and broken: it appears to have had a conical central cusp and small posterior accessory cusp. P_4 is complete, the tip of the cusp is somewhat worn and its anterior and posterior borders become slightly concave towards the base, with a prominent posterior cingulum around the accessory cusp. M_1 is missing and M_2 broken with only the base remaining; this indicates a strong paraconid-protoconid shear, slightly oblique, behind which lay a small antero-medially sloping talonid. M_3 is complete and indistinguishable from that on the holotype; the tooth is fully erupted in a crowded jaw, and lies obliquely resulting in a transverse shear.

Specimen CMF.4022 contains a M_3 with broken protoconid, but otherwise little worn. The fully erupted tooth in situ has an oblique shear, which runs at 40° to the longitudinal axis of the tooth row. CMF.4023 comprises a very broken tooth stump which is referred to the species on size, absence of talonid and metaconid, and obliqueness of shear.

Andrews (1906) referred a specimen (C.8812-13) from the Fluvio-marine beds north of Birket-el-Qurun in the Fayûm, to the genus *Hyaenodon*. On page 219 he described this right mandibular fragment and associated M_3 . The tooth is structurally indistinguishable from the holotype described above and nearly the same size. Nothing debars the specimen from inclusion in the species *H. andrewsi*.

***Hyaenodon (Isohyaenodon) matthewi* sp. nov.**

(Text-figs. 41-43)

DIAGNOSIS. *Isohyaenodon* of rather smaller size than *H. (I.) andrewsi* and M_3 with less oblique shear; details in accompanying table.

Trivial name is a tribute to W. D. Matthew, a British geologist whose signal contributions to mammalian palaeontology are unsurpassed.

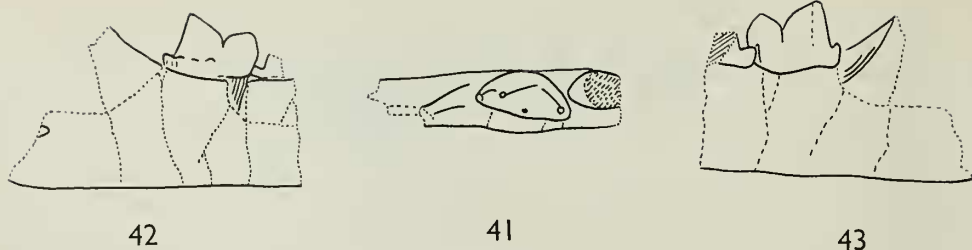
HOLOTYPE. M.19098. Left mandibular fragment with M_3 and broken M_2 from Songhor, Kavirondo Gulf, Kenya.

OTHER MATERIAL. The following additional specimens are referred to the species:

CMF.4060 Left M_2 from Rusinga Island, Kavirondo Gulf, Kenya.

CMF.4061 Right M_3 from Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION. A fragment of mandible surrounding M_3 is preserved. The build of the jaw is lighter than in *H. (I.) andrewsi*; the masseteric fossa is pronounced and a groove is present on the lower anterior face of the coronoid crest. M_3 is similar to that on *H. (I.) andrewsi* but proportionately smaller. The protoconid is higher than



FIGS. 41-43. *Hyaenodon (Isohyaenodon) matthewi* sp. nov. Left mandible with M_{2-3} . (41) Occlusal aspect. (42) Medial aspect. (43) Lateral aspect. Holotype (M.19098), Songhor. $\times 1$.

the paraconid and the shear plane convex outward; the obliqueness of shear is 20° , that is much less than in *H. (I.) andrewsi*. A vestige of the talonid is present and on this unworn tooth a very minute prong is visible on the internal cingulum at about the place where a metaconid would arise if one was present. The small talonid of M_2 abuts against the paraconid of M_3 , the alignment being maintained by a small buttress; no more of M_2 is preserved on the holotype.

On a left M_2 (CMF.4060) from Rusinga the protoconid is decidedly higher than the paraconid and a small talonid is present; the shear plane is convexly curved and not as oblique (at 15°) as that of M_3 . CMF.4061 is an isolated right M_3 , indistinguishable from the holotype, but slightly broken on the cusp tips.

Hyaenodon (Isohyaenodon) pilgrimi sp. nov.

(Text-figs. 44-49)

DIAGNOSIS. Small species of *Isohyaenodon*; about half the size of *H. filholi* and *H. mustelinus*.

The trivial name is a tribute to G. E. Pilgrim (1874-1943), an outstanding scholar of European and Asiatic Tertiary mammals.

HOLOTYPE. M.19100a-c. Pair of complete mandibles with posterior fragment of skull and 7 cervical vertebrae; from Rusinga Island, Kavirondo Gulf, Kenya.

OTHER MATERIAL.

CMF.4062 Right mandible with P_4 , M_{2+3} . Rusinga Island, Kavirondo Gulf, Kenya.

CMF.4063 Left mandible fragment with P_{2+4} , M_1 . Rusinga Island, Kavirondo Gulf, Kenya.

CMF.4064 Upper left M^1 . Songhor, Kavirondo Gulf, Kenya.

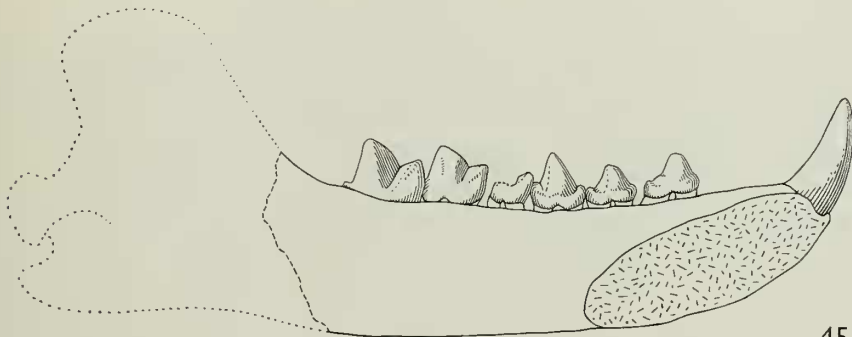
CMF.4065 Left lower canine. Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION. This species is about the same size as the polecat, *Mustela putorius*. The two mandibles are complete though separate and only the incisors and P_1 are missing. The mandible is about the same size as that of a pine marten; it is lightly built with a long symphysis. The coronoid is high and the crest rounded. The condyle is transverse, well rounded and on a level with the tooth row; below is the

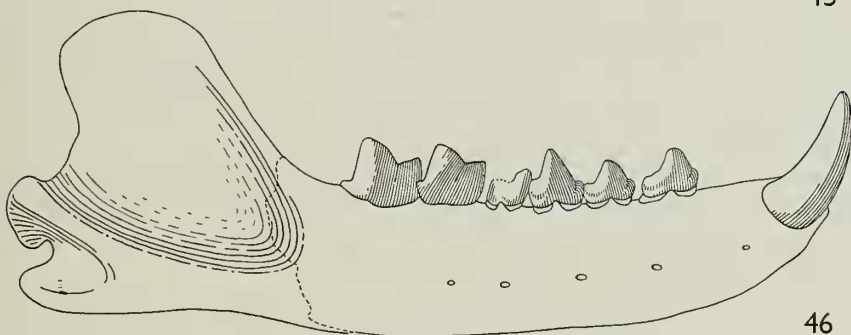
short stout angular process. The masseteric fossa is not deep and the mandibular foramen issues just posterior to M_3 . On the labial side of the jaw there is a row of mental foramina, below P_2 , P_3 , M_1 and M_2 .



44



45

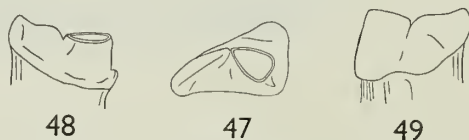


46

FIGS. 44-46. *Hyaenodon (Isohyaenodon) pilgrimi* sp. nov. Partial reconstruction from right and left mandible with C, P_2 - M_3 . (44) Occlusal aspect. (45) Medial aspect. (46) Lateral aspect. Holotype (M.19100), Rusinga Is. $\times 2$.

No incisors are known and from the proximity of the canine to the symphysis they must have been very small. The canine is slightly flattened on the medial side and tapers upward with a gentle curve backwards. P_1 is absent on both sides, and was apparently a small single-rooted tooth. P_2 is two-rooted, the cusp is centred over the anterior root and it slopes backward to a small accessory cusp over the posterior root. On P_3 the cusp is centrally placed, with a longitudinal keel running anteriorly to a slight cingulum and posteriorly to a small accessory cusp. P_4 is similar structurally to P_3 only slightly larger. M_1 is broken on both sides, but was clearly a small obliquely shearing molar, with protoconid rather larger than the paraconid and a vestigial talonid. M_2 is similar to M_1 but considerably larger and M_3 is slightly larger than M_2 . On M_3 the well developed shear is oblique, the proto-

conid is higher than the paraconid and the only trace of the talonid is a slight bump of enamel on the posterior edge of the protoconid. A minute buttress is present on the antero-labial edge of M_2 and M_3 . A left M^1 from Songhor is referred to the species.



FIGS. 47-49. *Hyaelodon (Isohyaenodon) pilgrimi* sp. nov. Left M^1 . (47) Occlusal aspect. (48) Lateral aspect. (49) Medial aspect. (CMF.4064), Songhor. $\times 4$.

Together with the two mandibles, the posterior part of the brain-case and seven cervical vertebrae are preserved; all are broken and partly crushed, particularly the posterior part of the skull, so that of this no details can be discerned.

In size and build the cervical vertebrae approach those of *Mustela putorius*, the polecat. The atlas vertebra possesses a fairly wide dorsal and narrow ventral arch, the latter with well developed longus colli tubercle. No rectus capitis posticus minor muscle scar is visible on the anterior face of the dorsal arch. The wings, though broken, can be seen to be light and did not project far laterally, no more than one third the width of the neural arch. The oblique foramen issues dorsally behind the cotylar process. The vertebrarterial canal is very short, the ventral and posterior openings being close together at the base of the wing. The axis is closely comparable with that of the polecat, and differs from it only in having light non-tuberculate posterior zygapophyses and the posterior extension of the spine beyond the neural arch, though broken, was probably thinner and shorter.

The remaining cervical vertebrae are partially crushed, especially on lateral and ventral faces. Their dorsal surfaces reveal that the neural spines were vestigial on third to fifth inclusive; the sixth cannot be seen and on the seventh a small spine was present.

The close comparison in size and proportions of the jaws and vertebrae with those of the polecat is instructive. In appearance *Isohyaenodon pilgrimi* must have looked very like a polecat, but perhaps without the latter's strength and agility. There is a consistent weakness in the development of dorsal musculature, a feature found in modern aquatic carnivores.

REMARKS ON *ISOHYAENODON* SPECIES

The most striking thing about the three new species is their similarity to each other and difference from other *Hyaelodon* species. Secondly the *Isohyaenodon* material falls readily into three groups on basis of size differences. The only other described species from Africa, *H. brachycephalus* can be included in the subgenus *Isohyaenodon* on the basis of near equality of paraconid and protoconid on M_3 . Its size is greater than any of the three species described above, and it possesses a relatively short mandible compared with others in the subgenus. The distribution of this character of mandibular length is another variable in the genus, which on available material, does not form any meaningful pattern.

TABLE 7. Measurements (in mm.) on *Hyænodon (Isokyaenodon)* species.

		M ¹		P ₁ -P ₄		M ₁ -M ₃		P ₂		P ₃		P ₄		M ₁		M ₂		M ₃	
		a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs	a-p	trs
<i>H. (I). andrewsi</i>	M.15048					36.6								8.9	4.1	12.0	6.0	15.4	7.5*
"	CMF.4021					38.0*				11.2		11.3		5.5		12.9		15.4	8.6
"	CMF.4022																	15.3	8.4
"	CMF.4023																	14.0*	7.3
"	C.8812-3																	13.0	7.0
<i>H. (I). matthewi</i>	M.19098																	12.7	6.2
"	CMF.4060															11.8		5.8	
"	CMF.4061																	12.8	6.7
<i>H. (I). pilgrimi</i>	M.19100		left			14.8	14.3	3.8	2.1	3.4	1.8	3.8	2.3	3.4	1.3	5.4	2.2	5.8	3.0
"	CMF.4062		right			—	14.3	—	—	3.4	1.4	3.6	1.8	3.5	1.7	4.9	2.3	5.8	2.7
"	CMF.4063											4.1	1.9			5.0	2.5	6.0	3.2
"	CMF.4064							3.4*	1.8			3.8	2.0	3.4	1.7				
		4.5	3.0																
<i>H. (I). brachycephalus</i>	Amer. Mus. No. 13264					32.3	33.7											19.0*	

*approximate.

Suborder FISSIPEDA Blumenbach

Superfamily *CANOIDEA* SimpsonFamily *CANIDAE* Gray

DIAGNOSIS. Arctoidea, with a moderately high skull, brain-case not expanded; auditory bulla originally small, remote from the paroccipital process, as in Amphicyoninae, but in most lineages ultimately becoming enlarged and inflated and brought into contact with the paroccipital process; alisphenoid canal present. Dental formula $\frac{3.1.4.3-2}{3.1.4.3-2}$: P^4 elongate, protocone prominent in early genera, later much reduced; M^1 3- or 4-tubercular, often with intermediate cusps, always broader than long, becoming progressively larger along many lines; M^2 similar, only very exceptionally lost; M^3 present in some early genera, and in most of the Amphicyoninae; lost later; M_1 with metaconid strong in primitive genera and in the Amphicyoninae, progressively weaker along other lines; talonid with trenchant hypoconid; entoconid present either as a ridge, shelf, or tubercles in the early genera, and retained on most lines; M_2 long; M_3 only exceptionally lost in some highly specialized genera; digitigrade; primitive members with five digits, later forms with first digit both in manus and pes reduced. [after Pilgrim 1931].

REMARKS. About 60 genera of fossil canids are recognised and in addition there are 12 living genera. The classification of these numerous genera within the family Canidae presents many difficulties and numerous attempts have been made. None is completely satisfactory. The relative abundance of fossil forms increases rather than lessens the difficulties. Simpson (1945) has stated of the Canidae that their "status as a single family . . . can be upheld without serious doubt" and then adds "the whole group is extremely polyphyletic"—two statements which appear irreconcilable. It is beyond the scope of this work to attempt yet a further revision of the classification (a task begun by Hough (1948) for American fossil genera and by Hürzeler (1944) and Ginsburg (1955) for some of the European genera): It will suffice here to adopt the status of the subfamily Amphicyoninae as defined below, without reference to its relationship to other subfamilies.

Subfamily *AMPHICYONINAE* Trouessart

DIAGNOSIS. Canidae, with auditory bulla small, little inflated, remote from the paroccipital process; mastoid process prominent and broad; molars progressively enlarged, premolars and carnassials progressively reduced; upper molars tritubercular, with broad postero-internal shelf; M^3 and M_3 present in most forms, but lost in advanced members; P^4 with progressively reduced protocone; M_1 generally with metaconid, talonid with hypoconid and ridged entoconid. M_2 with bicuspid trigonid and crested talonid; limb bones massive; humerus with entepicondylar foramen; manus and pes 5-dactyl. [after Pilgrim 1931.]

REMARKS. Only one genus (*Mammocyon* Loomis 1936) has been added to the subfamily since Pilgrim (1931) discussed its status. Arambourg (1961) described a very worn mandibular fragment from Gebel Zeltan in Libya as *Afrocyon*, a new genus

of amphicyonid. Until more material is available nothing useful can be added to this statement. In the confusion that exists regarding the affinities of the canid genera, it would be futile to attempt a concise formulation of any one subfamily. The new genus described below is included with the Amphicyoninae on the basis of its close parallels to *Amphicyon*, rather than on a rigorously definitive basis. When canid systematics are usefully revised, the two genera will probably be placed close together.

Genus *HECUBIDES* nov.

DIAGNOSIS. Amphicyonine with long face; dental formula $\frac{3.1.4.3}{3.1.4.3}$; anterior premolars well spaced; P^4 reduced in comparison with molars; protocone not so anteriorly placed as in *Amphicyon* and parastyle absent; carnassial blade not oblique; M^1 only slightly larger than M^2 ; both sub-triangular and transverse width greater than length, lunate protocone and extensive internal cingulum more asymmetrical and smaller on M^1 ; paracone and metacone equal on M^2 and metacone only slightly smaller than paracone on M^1 . M^3 small: M_1 with well developed trenchant hypoconid and ridged entoconid.

TYPE SPECIES. *Hecubides euryodon* sp. nov.

In addition to the type species a second new species, *H. macrodon*, is described below and two others are referred to the genus, *H. americanus* (Wortman) and *H. lemanensis* (Pomel).

REMARKS. The probable affinities of the new genus are described below in the remarks on the type species. It is quite distinct from both the European *Amphicyon* and the American *Daphoenus* and appears to represent a separate stream of development.

Hecubides euryodon gen. et sp. nov.

(Pl. 5, fig. 1; Text-figs. 50-54)

DIAGNOSIS. Medium sized *Hecubides* species: M^1 about 18 mm. transversely and 15 mm. longitudinally: M^1 with strong internal cingulum, no crenulation on either protocone or internal cingulum of either M^1 or M^2 .

DERIVATION OF NAME. Generic name from Hecuba, princess in Greek mythology who was changed into a stone dog. The trivial name is from the Greek *eury*s, wide or broad.

HOLOTYPE. M.19084. Maxillary fragment with P^{3+4} , M^{1+2} and alveoli of P^2 and M^3 on both sides.

LOCALITY. Locality I, Napak, Karamoja, Uganda.

PARATYPE. In addition to the holotype, the type locality has yielded an isolated right M_1 (M.19085).

ADDITIONAL MATERIAL. The following specimens are referred to the species:—

M.14313	Right M ¹ , broken	Koru, Kavirondo Gulf, Kenya.
M.19099	Left M ₁	Locality I, Napak, Karamoja, Uganda.
CMF.4026	Right M ₁	Songhor, Kenya.
CMF.4027	Right M ₂	Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4067	Left M ₁ , talonid only	Rusinga Island, Kavirondo Gulf, Kenya.
CMF.4068	Left M ₂ , protocone only	Mfwanganu Island, Kavirondo Gulf, Kenya.
CMF.4069	Left M ₁ , trigonid only	Rusinga Island, Kavirondo Gulf, Kenya.
H.M.V.5830	Left M ₁	Locality IV, Napak, Karamoja, Uganda.
UMP64.32	Right M ₂	Locality I, Napak, Karamoja, Uganda.

DESCRIPTION. The holotype consists of an incomplete maxillary dentition together with the adjacent parts of the maxillae bones. P⁴, M¹⁺² are preserved on both sides: P³ is complete on the right side, broken on the left: parts of the alveoli of P² and M³ can be distinguished. The dentition gives an overall impression of robustness; the teeth have thick enamel, low cusps and are relatively wide.

The premolar teeth are well spaced and indicate a relatively long but strong jaw. Nothing anterior to the alveolus of P² is known; of this tooth only the posterior root cavity remains and it was presumably a smaller version of P³ which is a single cusped birooted tooth, narrow and elongated. In P⁴ the fully sectorial paracone-metastyle blade is directed antero-posteriorly; the paracone is higher and larger than the metastyle and the two are separated by a narrow cleft: no parastyle is present, though a slight bump can be detected on the ridge of enamel which falls anteriorly from the summit; the protocone is small, low, close to the paracone and lies midway between the paracone summit and its anterior border. M¹ is a large triangular tubercular tooth, with its transverse width greater than its length; the paracone is slightly larger than the metacone and both have prominent antero-posterior keels. The crescentic protocone, separated by a wide basin from the paracone and metacone, is slightly asymmetrical, being shorter but heavier anteriorly; lingual to the protocone is a thick cingulum, and a narrow cingulum runs buccal to the paracone and metacone. M² is only slightly smaller than M¹ and structurally very similar; the protocone is symmetrical and less high than in M¹ and the lingual cingulum is larger and more expanded. The only evidence of M³ is a trace of the alveolus indicating a small, transverse two rooted tooth.

Mandibular teeth referred to the species are first and second molars. M₁ is a robust tooth, the trigonid is about twice as long as the talonid; paraconid and protoconid are sectorial, protoconid is much the largest cusp; the metaconid is small, adhering

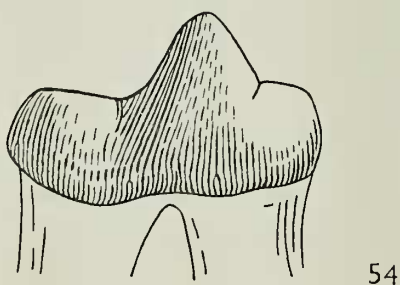
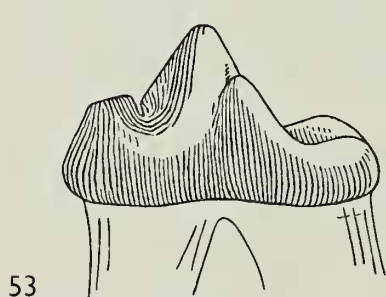
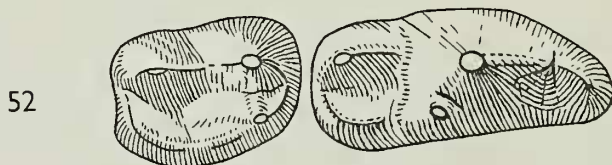
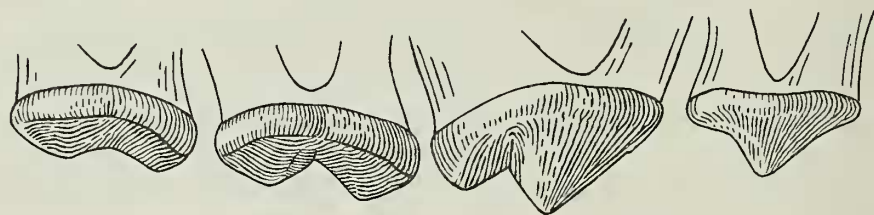
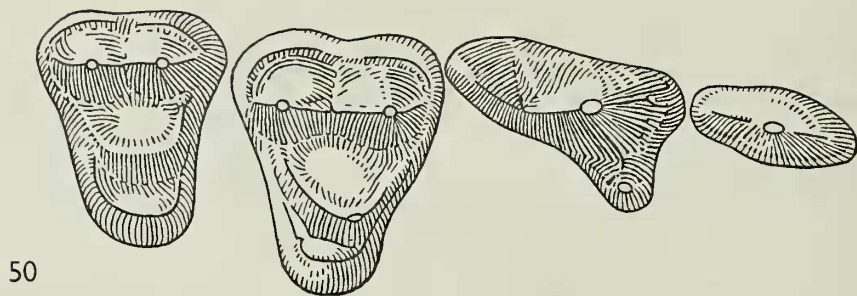
to the protoconid with crest on level of the paraconid; the talonid is basined, length and breadth about equal, hypoconid well developed and entoconid forms a low ridge. M_2 is a stout rectangular tooth; the prominent protoconid is paired with a smaller metaconid and there is no paraconid; posteriorly the hypoconid is keeled and continues in line with the protoconid; the entoconid presents a curved ridge linking the paraconid and hypoconid.

The other specimens do not call for any special comment. Most are M_1 and few are unbroken.

REMARKS. *Hecubides* is known from three sites in the Kavirondo region of Kenya and from Karamoja in Uganda. These, with *Afrocyon* from Libya, are the earliest records of canids in Africa, the next being *Canis* and *Vulpes* in the Lower Pleistocene. In comparing *Hecubides* with other canids, we may limit study to those genera grouped by Simpson (1945) in the subfamilies Caninae, Amphicyonodontinae and Amphicyoninae. The American subfamily Borophaginae is quite different and need not be considered: the octocyoninae, with one living African genus and two possible Pleistocene precursors, has very atypical molar characters: all simocyonines are characterised by the absence of M^3 and very reduced M^2 .

Of the numerous American canid genera, none is as close to *Hecubides* as some European *Amphicyon* species. The following characters clearly differentiate the American canids: many are either without M^3 (as *Nothocyon*, *Cynodesmus*, *Mammocyon* and *Pliocyon*) or the tooth is very reduced as in *Proamphicyon*: in most genera M^2 is considerably smaller than M^1 (e.g. *Hesperocyon*, *Daphoenus* and *Campylacynodon*): the development of the protocone on P^4 is large with poor or oblique shearing blade in *Daphoenus* and *Daphoenodon*; the protocone is small and the blade strongly sectorial in *Mesocyon* and *Mammocyon*: the metaconid is a free and fully developed cusp in the M^1 of *Daphoenus* and *Parictis*, and the talonid has high entoconid and hypoconid cusps in *Tomarctus* and *Leptocyon*: a paraconid is present on M_2 in *Leptocyon* and *Tephrocyon*. Omitting the oasis of synonyms, and other genera either so different or so poorly known that they do not warrant discussion, only the American species referred to *Amphicyon* remain and these are discussed below together with the old world species.

Among the European Tertiary canids, the closest affinities with *Hecubides* are to be found among the *Amphicyon* group. Among the *Hemicyon* group of genera (*Hemicyon*, *Harpalaeocyon*, *Dinocyon*, *Plithocyon*, *Phoberocyon*) there are fairly close similarities in the structure of the upper and lower molars, but all are more specialised for crushing; the teeth are more tuberculose, the upper molars wide and almost square in some cases, the protocone of P^4 large and medianly placed. The essential differences between *Hecubides* and the remaining genera can be briefly listed: *Cynodictis* (with *Plesiocyon* and *Pachycynodon*) possesses viverrid-like characters—very reduced M^2 and high tricusped trigonid on M_1 ; *Cephalogale*, *Alopecodon* and *Pseudamphicyon* all lack M^3 and have reduced M^2 ; *Amphicyonodon* (synonyms *Cynodon* and *Paracynodon*) has tricusped trigonid on M_1 and a paraconid is present on M_2 .



FIGS. 50-54. *Hecubides eurydon* gen. et sp. nov. (50) Maxilla with P³-M¹, based on the right and left sides of dentition; occlusal aspect. Holotype (M.19084), Napak. (51) same, lateral aspect. (52) M₁ and M₂, based on M.19085, M.19099 and CMF.4027; occlusal aspect. (53, 54) M₁, based on M.19085 and M.19099; medial and lateral aspects. All $\times 2$.

Only two additional genera require examination to survey the Asiatic Tertiary canids. *Vishnucyon* bears no resemblance whatever to *Hecubides*; its P^4 is without a protocone, the M^1 is deeply waisted and M^2 very reduced. *Arctamphicyon*, known from M^{1+2} , suggests ursid affinities in its narrow but transversely extended molars.

The type species of *Amphicyon* is *A. major* Blainville. This species is clearly generically distinct from *Hecubides*, the most striking differences being in M^2 , which on *Amphicyon major* is asymmetrical transversely, has a crenulated internal cingulum and the paracone is much larger than the metacone: the molar teeth are subsquare rather than sub-triangular and the internal cingulum is less extensive in both teeth than in those of *Hecubides*. All four premolars are present though P^1 is vestigial and there is a diastema between it and the canine, which reaches the proportions of a sabre-tooth: the diastema behind the upper canine suggests further an elongate lower canine. The asymmetry of the buccal border of M^2 and the striking difference in size of paracone and metacone, are features which clearly mark off the *Amphicyon* group from *Hecubides*.

About 70 species have been referred to the genus *Amphicyon*. Apart from a profusion of synonyms it is clear that several genera are involved and some of the species bear little resemblance to the type species. Only those which are clearly nearer to the genus *Hecubides* than to the type species *A. major* will be discussed below. None of the eight Asiatic species of *Amphicyon* come within this category. Of the 18 American species attributed to *Amphicyon*, *A. americanus* more closely resembles *Hecubides* than *A. major*. I have been able from a cast to confirm Matthew's remarks (1924: 106) that *A. sinapius* is closer to *A. major* than to *A. lemanensis* and has no proximity to *Hecubides*. None of the other American species comes within the scope of the discussion and only *A. americanus* is transferred to the new genus *Hecubides*.

Among the European *Amphicyon* species, *A. lemanensis* stands out as quite distinct from all others, and close to *Hecubides euryodon*. Both species are about the same size; P^4 , M_{1+2} are almost identical in each, M^1 of *A. lemanensis* has a crenulated protocone and the postero-internal cingulum is much larger and more asymmetrical, while the M^2 is proportionately broader transversely and the external border is directed postero-internally. Both species are undoubtedly closely allied and the European species is thus placed in the new genus. *A. dehmi* Crusafont, from the Burdigalian of Vallés-Penedés, N.E. Spain appears to fall between *Hecubides* and *Amphicyon*. The rather squarish molars, M^1 slightly asymmetrical, M^2 with posteriorly crenulated internal cingulum and a paracone which is slightly larger than the metacone tend to suggest a closer proximity to *Amphicyon sensu stricto*. Crusafont (1955) has justifiably placed the species in a new subgenus *Ictiocyon* of the genus *Amphicyon*.

In conclusion therefore, the new genus *Hecubides* has four known species, the type species *H. euryodon* and another new one from East Africa, *H. macrodon*. To these are added *H. americanus* (Wortman) from Nebraska (age unknown), and *H. lemanensis* (Pomel) from the Aquitanian of France and Germany. *Hecubides* appears to be

an earlier offshoot of the dogs than *Amphicyon*: the latter could be said to be more specialised in having molars more nearly square than triangular, a more elaborate internal cingulum on M^2 and a greater development of the paracone at the expense of the metacone.

Hecubides macrodon sp. nov.

(Pl. 5, fig. 2; Text-fig. 55)

DIAGNOSIS. Large sized *Hecubides* species; M^1 about 25 mm. transversely and 20 mm. longitudinally; internal cingulum proportionately smaller and external cingulum thinner than in type species.

HOLOTYPE. M.19086. Left M^1 .

LOCALITY. Site 31, Rusinga Island, Kavirondo Gulf, Kenya.

DESCRIPTION. M^1 is structurally similar to that of *H. euryodon*, but larger, with rounded and less pronounced features. The paracone is slightly wider than the metacone: the protocone forms a broad and shallow crescent and the internal cingulum, best developed posteriorly, is proportionately smaller than in *H. euryodon*: the external cingulum is very thin and forms only a skin on the lower edges of the paracone and metacone.

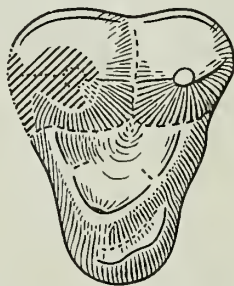


FIG. 55. *Hecubides macrodon* sp. nov. Left M^1 ; occlusal aspect.
Holotype (M.19086), Rusinga Is. $\times 1.5$.

REMARKS. Few deductions can be made from an isolated tooth, but its difference from *H. euryodon* in size and minor details of structure, seem sufficient to merit specific distinction. The remarks on the type species regarding the relationships to *Amphicyon* apply also to this species.

A right P^4 (CMF.4070) from Rusinga is also referred to *H. macrodon*; the tooth is very broken and only the outer edge of the paracone and metastyle survive.

TABLE 8

Measurements (in mm.) on the dentitions of *Hecubides*.

		P ³	P ⁴	M ¹	M ²	M ³	M ₁	M ₂
<i>Hecubides euryodon</i>								
P ³ -M ² M.19084 (Holotype)	a-p	11.3	17.5	14.6	12.9	—	21.3	13.7
M ₁ M.19085 (Paratype)								
M ₂ CMF.4027	trs	5.3	10.3	17.5	16.4	—	9.6	10.3
<i>Hecubides euryodon</i>	a-p						23.5	
Hunt. Mus. V.5830	trs						9.9	
<i>Hecubides macrodon</i>	a-p			20.5				
M.19086								
(Holotype)	trs			24.2				
<i>Hecubides americanus</i>	a-p	15	27	20	17	8		
(Wortman)								
(Holotype, approx.)	trs	8	17	27	22	12		
<i>Hecubides lemanensis</i>	a-p		17.4	14.5				
(Pomel)								
(B.M.N.H., no. 30879)	trs		10.3	18.4				
<i>Hecubides lemanensis</i>	a-p			15.1	12.0			
(Pomel)								
M.7643	trs			19.5	17.2			
<i>Hecubides lemanensis</i>	a-p						20.1	
(Pomel)								
(B.M.N.H., no. 26733)	trs						9.1	
<i>Amphicyon (Ictiocyon)</i>	a-p		16.6	15.6	11.5	7.4	18.0	
<i>dehmi</i> Crusafont								
(Holotype)	trs		12.1	17.5	16.4	11.7	9.7	
<i>Amphicyon major</i> de								
Blainville	a-p		32.3	27.1	22.4			
(B.M.N.H., no. 29615)								
(Cast of holotype)	trs		19.2	35.0	31.7			

Superfamily **FELOIDEA** SimpsonFamily **VIVERRIDAE** Gray

DIAGNOSIS. Skull elongate, low with long snout; auditory bulla composite with ecto- and ento-tympanic parts, wholly or only partially ossified. Dental formula $\frac{3.1.4.2}{3.1.4.2}$: M¹⁺² large, tritubercular: P⁴ with well developed protocone; parastyle and metastyle usually present: M₁ long with tritubercular trigonid and basined talonid; trigonid cusps usually high; carnassial P⁴/M₁, truly sectorial except in few specialized genera. [After Pilgrim 1931].

REMARKS. On teeth alone it is impossible to separate with certainty the miacids from the viverrids and the auditory region is essential for this purpose. This region is missing from the specimens described below and hence their place in the Viverridae must be regarded as provisional. The later miacids and early viverrids are so similar that it is impossible to make a sharp division. Gregory & Hellman (1939) included miacids within their family Viverridae though this practice has not been generally accepted. The miacid subfamily Viverravinae is closest to the Viverridae, all its members lacking M_3 as in viverrids. Simpson (1945) recognised seven subfamilies in the Viverridae, of which only three, Stenoplesictinae, Viverrinae and Herpestinae are known in the fossil record: the latter two subfamilies contain half the 42 recognised genera in the family.

Subfamily **HERPESTINAE** Gill

DIAGNOSIS. External auditory meatus long. Carnassial teeth not strongly trenchant; molars rather more sectorial than tubercular.

REMARKS. The Herpestinae are essentially less specialized in the carnassial direction than the Viverrinae, though the trenchant character of the teeth is not so reduced as in Paradoxurinae and Hemigalinae. It is on this basis that the fossils described below are included in the Herpestinae, in lieu of any knowledge of the auditory region. No extinct genera are ascribed to the subfamily and only *Herpestes* among the ten genera listed by Simpson (1945) has a fossil record, which in Europe extends into Upper Oligocene. The lack of differentiation of distinct fossil genera reflects difficulties of establishing diagnostic characters.

Genus **KICHECHIA** nov.

DIAGNOSIS. Herpestine with upper dental formula 3.1.4.2. Teeth not compressed; canine long and slender; parastyle present only on P^4 ; upper molars without conules and without hypocone; protocone crescentic and without anterior and posterior wings.

TYPE SPECIES. *Kichechia zamanae* sp. nov.

REMARKS. Only the holotype and isolated teeth or partial dentitions are known and they possess no characters which would preclude them from the Viverravinae. The sum of the dental characters is diagnostic, though individually several of them are to be found in other genera.

Kichechia zamanae gen. et sp. nov.

(Pl. 5, fig. 3; Text-figs. 56–60)

DIAGNOSIS. The only known species, diagnosis as for genus.

The name is derived from the Swahili word *kichechi*, a mongoose, and *zamani* meaning ancient.

HOLOTYPE. *M.*19077*a*, *b*. Facial region of skull and anterior part of braincase with complete upper dentition on right side except P^1 .

LOCALITY. Site R 1, Rusinga Island, Kavirondo Gulf, Kenya.

PARATYPES.

- M.19078 Right mandible with Canine root; P_{2-4} ; root of M_1 . Site 2, Rusinga Island.
 M.19079 Right M_1 . Rusinga Island, Kavirondo Gulf, Kenya.
 M.19080 Right mandible with P_4 ; M_{1-2} . Songhor, Kenya.

ADDITIONAL MATERIAL.

From Rusinga Island, Kavirondo Gulf, Kenya.

- CMF.4003 Right M^1 .
 CMF.4004 Left M^1 and alveolus of P^4 . Site 12.
 CMF.4006 Left mandible with C root, P_1 alveolus, P_{2-4} , M_1 . Site 1.
 CMF.4008 Left mandibular fragment with P_4 , M_1 .
 CMF.4009 Left mandibular fragment with C, P_1 roots, P_{2-4} .
 CMF.4010 Left mandibular fragment with M_1 . Site 1.
 CMF.4011 Right mandibular fragment with P_4 , M_1 ; roots of P_{2-3} and M_2 . Site 1.
 CMF.4012 Right mandibular fragment with P_{2-4} , M_1 ; roots of P_1 and C.
 CMF.4014 Right M_1 .
 CMF.4015 Right mandibular fragment with P_{3-4} , M_1 ; roots of P_2 and M_2 .
 CMF.4016 Right mandibular fragment with P_4 , M_1 ; roots of P_3 and M_2 . Site 1a.
 CMF.4017 Right mandibular fragment with P_4 ; roots of M_{1-2} .
 CMF.4029 Right mandibular fragment with P_4 , M_1 ; roots of M_2 . Site 1.
 CMF.4030 Left mandibular fragment with M_1 , broken P_4 .
 CMF.4031 Left mandibular fragment with P_4 and broken M_1 .
 CMF.4032 Left mandibular fragment with M_1 ; root of M_2 .
 CMF.4033 Left mandibular fragment with P_{1-4} .
 CMF.4034 Left M_1 . Site 6.
 CMF.4035 Right M_1 .
 CMF.4036 Right P_4 .
 CMF.4037 Left P^4 . Site 1.
 CMF.4071 Right maxillary fragment with P^4 , M^1 2.
 CMF.4072 Left P^4 .
 CMF.4074 Left upper canine.
 CMF.4075 Left mandibular fragment with P_4 , M_1 .
 CMF.4076 Left mandibular fragment with P_3 .
 CMF.4077 Left M_1 in mandibular fragment.
 CMF.4078 Left P_{1-3} in mandibular fragment.

From Mfwanganu Island, Kavirondo Gulf, Kenya.

- CMF.4005 Right M^1 .

From Moruorot, Northern Frontier District, Kenya.

- CMF.4013 Right mandibular fragment with P_1 root, P_{2-4} , M_1 .

From Songhor, Kenya.

CMF.4073 Anterior facial region of skull with nasals, maxillae, frontals, palatines; no teeth.

From Napak, Karamoja, Uganda.

UMP64.35 Left mandibular fragment with C and roots of P_{1-4} . Napak V.

UMP64.34 Right M_1 . Napak IV.

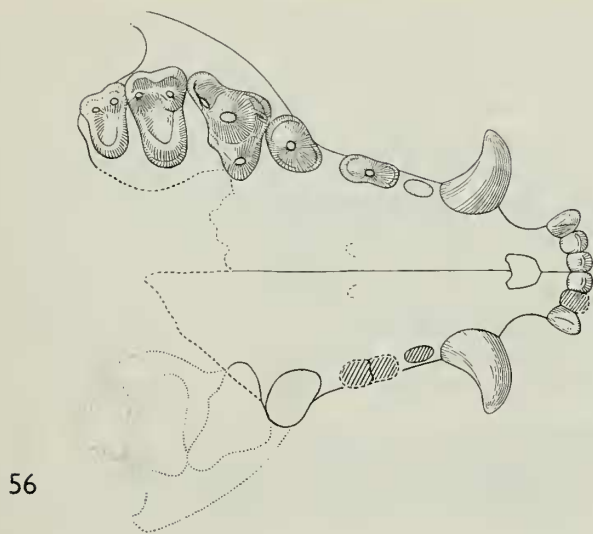
DESCRIPTION. In the holotype the facial region of the skull is complete but is broken off about the fronto-parietal junction and the whole of the posterior is missing. The skull is fractured and partly displaced, but may have had size and proportions similar to a living mongoose.

The face is long, low and narrow. The premaxilla has a long, tapering ascending ramus which reaches back to the line of P^1 . The maxilla is almost wholly vertical on its outer face and posteriorly carries the stout base of the zygomatic arch: the infra-orbital foramen is smaller than the canine alveolus and lies almost immediately above P^3 . The frontal bones are flattened dorsally. The extremities of the post-orbital processes are broken on each side, but from their roots it can be judged that they were well developed: since the zygomaxilla is broken off near its anterior root, it is not possible to estimate how fully the orbit was enclosed posteriorly. From the postorbital process a ridge sweeps posteriorly toward the mid-line; these two ridges meet and continue medianly backward, but do not form a true sagittal ridge; the ridge indicates the upper limits of the origin of the temporal muscles and their meeting medianly suggests powerful musculature to the mandible. The skull is very constricted immediately behind the postorbital processes, narrowing to 9 mm. after which it expands rapidly to 20 mm. width; posteriorly to this it is missing. The anterior palatine foramen is about the size of the alveolus of I^3 , lying near the median plane between I^3 and C in the narrow pre-maxillary region. The posterior palatine foramina are smaller and lie opposite the posterior end of P_3 . The palatine bone is almost the same length as the palatine portion of the maxilla, extending backward 18 mm. from the anterior edge of P^4 : the pterygoid process is broken.

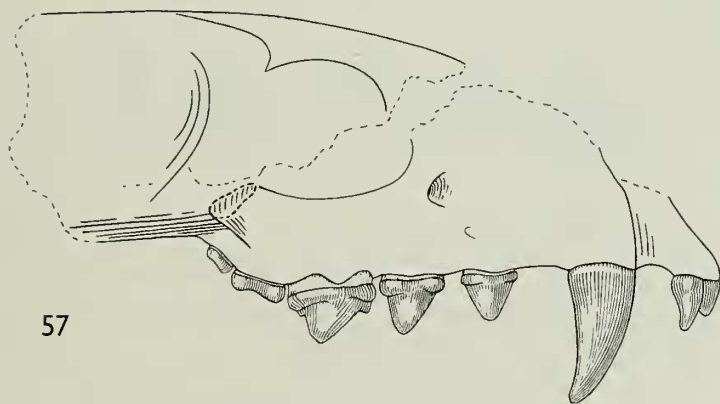
The horizontal ramus of the mandible is preserved in one of the paratypes (M.19078): the bone is slender in transverse section and relatively shallow dorso-ventrally compared with its length. The teeth are closely packed; a large mental foramen occurs below P_2 and there are several smaller ones posteriorly.

DENTITION. The dental formula is $\frac{3.1.4.2}{1.4.2}$. The holotype has all three incisors and the canine on each side, together with P^2 , $3+4$, M^{1+2} on the right side. The three incisors lie transversely on a slight curve, all close together, I^2 is slightly larger than I^1 , and I^3 is much larger than I^2 : I^1 and I^2 are spatulate. I^3 is conical with a groove cutting postero-buccally across it and worn by friction with a ridge on the antero-lingual border of the lower canine. A diastema 3.1 mm. long separates I^3 from C. The canine is long, slender, gently tapering and slightly curved: in transverse section it is ovoid, more flattened lingually than buccally: anteriorly the tooth is rounded and posteriorly keeled: there is a slight ridge on the antero-lingual margin.

P^1 follows immediately behind C without any gap: the tooth is absent on both



56



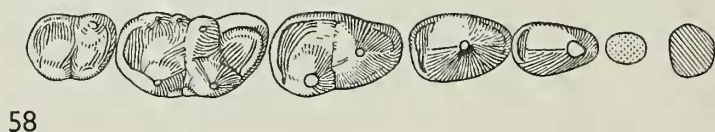
57

FIGS. 56, 57. *Kichechia zamanae* gen. et sp nov. Facial region, left and right sides united in reconstruction. (56) Occlusal aspect. (57) Lateral aspect. Holotype (M.19077), Rusinga Is. $\times 2$.

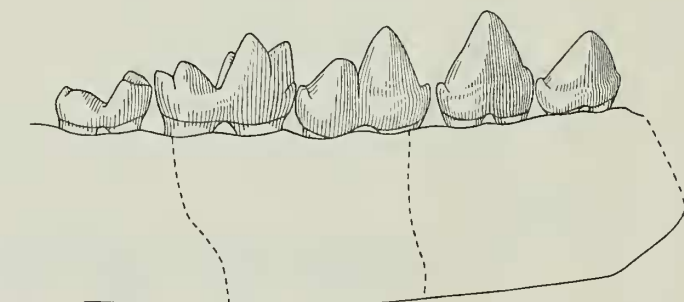
sides and only the small single alveolus remains. P^2 is a two-rooted tooth with single cusp, whose height is equal to its antero-posterior width at the level of the continuous basal cingulum. P^3 is slightly larger than P^2 ; cusp height is again equal to antero-posterior width at the base of the crown; the cingulum is continuous and most prominent posteriorly. P^4 is relatively broad and stout with the carnassial shear oblique: the large prominent paracone continues anteriorly into a small parastyle: the protocone is a low cusp, well developed; the metacone short and trenchant, intermediate in height between paracone and protocone: a cingulum is present buccally and posteriorly. M^1 is transversely broad; paracone and metacone are

equally developed; parastyle absent, but buccal cingulum present; protocone is symmetrical, crescentic, and bounded internally by a cingulum. M^2 is very similar to M^1 but smaller; cingulum less well developed. The continuity of bone behind M^2 testifies to the complete absence of M^3 .

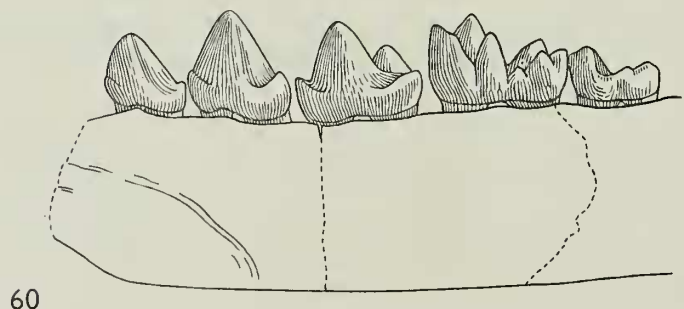
In the mandibular dentition no incisors are known. Only the root of the canine is preserved and this extends posteriorly under P_{1+2} . In section the canine is roughly ovoid at the base and smaller than the upper canine. P_1 is unknown, but the single small alveolus indicates an almost vestigial single cusped tooth. On P_2 the cusp is asymmetrical, more steeply inclined and smaller on the anterior half; a cingulum is present posteriorly and there is the trace of one anteriorly. P_3 is an enlarged version of P_2 ; its cusp height is approximately equal to its antero-posterior length; the posterior cingulum is well marked but the anterior one is small; a minute accessory cusp is sometimes present on the posterior keel of the main cusp. P_4 is larger than



58



59



60

FIGS. 58-60. *Kichechia zamanae* gen. et sp. nov. Mandibular dentition, P_2 - M_2 ; composite reconstruction based on M.19078, M.19079 and M.19080. (58) Occlusal aspect. (59) Lateral aspect. (60) Medial aspect. $\times 3$.

P_3 ; the main cusp rises to about the same level as that of P_3 and is steeper buccally than lingually; a small cingulum is present on the antero-lingual extremity. The posterior slope of the main cusp carries a prominent accessory cusp on the buccal side while postero-lingually is developed a low cingulum.

On M_1 the protoconid is the highest of the three cusps on the trigonid, with the paraconid more robust than and very slightly higher than the metaconid; the buccal border of the protoconid and paraconid is trenchant and the two cusps are separated by a deep notch: the talonid is about the same length as the trigonid; the prominent hypoconid is separated from the trigonid by a deep cleft and the lingual border of the talonid is fringed by a slightly crenulated cingulum. M_2 is present only on one specimen (M.19080) and on this is damaged: it is a small two-rooted tooth with apparent low protoconid and metaconid; the talonid is slightly larger than the rest of the tooth, carrying a hypoconid buccally which continues lingually as a low cingulum.

REMARKS. Among the living herpestines, the dentition of *Bdeogale* is closest to *Kichechia*, both animals being about the same size. In *Bdeogale*, I^3 is larger than in *Kichechia*, while the upper canine of the fossil genus is slightly larger and curved posteriorly unlike the straight canine of *Bdeogale*. P^3 in the living genus is large, with an internal cusp not found in *Kichechia*. P^4 is very similar in both genera, the metastyle being slightly larger and the protocone more anteriorly placed in *Kichechia*. The first upper molars are essentially similar, the fossil form having a slightly less prominent external cingulum and more prominent internal one. The proportion of M^1/M^2 is alike in the two genera.

In the mandibular dentition the premolars are similar, but the molars display differences. M_1 trigonid in *Bdeogale* is unusual, the metaconid being connate with the paraconid, and the protoconid and paraconid being separated by a trough, at the base of which arises an incipient cusp (paraconulid); the talonid has a prominent hypoconid: M_2 is proportionately much larger than in *Kichechia* with well developed trigonid and talonid. These differences in the lower dentition are striking, but two points of importance are first, the lower teeth referred to *Kichechia* are not associated with maxillary parts in the same specimen and hence their relationship is only an inferred one; secondly the mandibular molars of *Bdeogale* are highly exceptional, differing from other genera of herpestines.

The essential character of the dentition of *Kichechia*—the formula, tooth proportions, cusp development and degree of sectorial development—all suggest close affinity with Herpestinae. The Viverrinae are more specialized in the sectorial direction than the Herpestinae, but on dental characters alone *Kichechia* could represent the common stock from which both lines evolved. Comparison with the Miacidae, especially the Viverravinae, is valid in terms of dental formula and tooth structure, but differs in detail. *Kichechia* lacks the strong parastyle on M^1 and the high M_1 trigonid with weak talonid so characteristic of viverravines.

Kichechia has no close affinity with the Stenoplesictinae, the only other Tertiary viverrids. *Kichechia* is the earliest known example of a viverrid in Africa, the next record being in the Pleistocene.

TABLE 9

Dental measurements (in mm.) of *Kichechia zamanae*

		C	P ¹	P ²	P ³	P ⁴	M ¹	M ²
M.19077b	ant-post	4.1	—	4.0	4.4	6.6	4.4	3.2
	lat	2.8	—	2.2	3.7	6.0	6.9	5.4
CMF.4006				P ₃	P ₃	P ₄	M ₁	M ₂
	ant-post			3.8	4.5	5.6	6.5	
	lat			2.1	2.7	3.3	3.8	
M.19078	ant-post			3.6	4.4	5.8		
	lat			2.4	2.9	3.4		
M.19079	ant-post						6.7	
	lat						3.7	
M.19080	ant-post							4.0
	lat							2.8

Family **FELIDAE** Gray

DIAGNOSIS. "Aeluroidea, primitively with long skull, becoming progressively shorter, especially the face; rather inflated braincase; alisphenoid canal only present in primitive forms; entotympanic portion of auditory bulla very large, separated by a high septum (occasionally doubtfully so) from the laterally placed, smaller ectotympanic; external auditory meatus short; paroccipital process separated from the mastoid process, stretched out against the hinder part of the bulla; dental formula $\frac{3.1.3-2.1}{3.1.3-1.1}$: canines strongly developed; M₁ with two converging blades developed from paraconid and protoconid; primitive forms with strong metaconid, progressively becoming fused with protoconid, talonid only present in primitive forms, trenchant, progressively disappearing. M¹ and M₂ always small; premolar series progressively reduced; humerus usually with entepicondylar foramen; extremities relatively long and slender, digitigrade; manus 5-dactyl; pes generally 4-dactyl; claws retractile, except in *Acinonyx* and allied genera; os penis rudimentary." (Pilgrim 1931).

REMARKS. The division of the family into four subfamilies as given in Simpson (1945) is adopted here.

Subfamily **NIMRAVINAE** Trouessart

DIAGNOSIS. Felids with large incisors; upper canine enlarged and lower canine normal or slightly reduced; carnassial teeth deeply notched; P³ large, P⁴ with well developed protocone, strong paracone and parastyle present; anterior premolars absent or vestigial.

REMARKS. The large upper canines and incisors distinguish the subfamily less from the Felinae than the deep notches on the carnassial teeth distinguish it from the Machairodontinae. Scott & Jepsen (1936) erected the subfamily to accommodate *Archaelurus* and *Nimravus* and specifically excluding *Pseudaelurus* and *Metailurus*. Teilhard de Chardin (1945) suggested the erection of the subfamily Pseudaelurinae to accommodate *Pseudaelurus* and *Metailurus*. Simpson (1945) placed all the above

genera in the Nimravinae. The latter grouping is followed here giving a total of ten genera; *Ailurictis* and *Dinailurictis* from the European Eocene and Oligocene; *Dinictis*, *Nimravus*, *Dinaelurus*, *Archaelurus* and *Pogonodon* from the Oligocene and Lower Miocene of North America; *Pseudaelurus* from the Miocene of Europe and North America; *Metailurus* from the Upper Miocene of Europe and Asia. Kitts (1958) erected the genus *Nimravides* to accommodate the North American Pliocene species *Pseudaelurus thinobates*. The subfamily shows features in advance of the Proailurinae and probably includes ancestral stocks of both felines and machairodontines.

Genus *METAILURUS* Zdansky 1924

DIAGNOSIS. Nimravine with P^{1+2} absent, P^3 large and P^4 with strong paracone and well developed parastyle; P_2 if present very reduced.

TYPE SPECIES. *Metailurus major* Zdansky.

In addition to the type species, Zdansky (1924) described another species, *M. minor* from the same Pontian beds of China. Colbert (1939) described *M. mongoliensis* from the Vindobonian of Mongolia, and Thenius (1951) transferred *Felis leiodon* Weithofer to the genus as *M. parvulus*. Andrews (1914) described a mandible from Karungu, Kenya as *Pseudaelurus africanus* and below this is transferred to the genus *Metailurus*.

REMARKS. Matthew (1929: 496) wrote "*Metailurus* does not seem to me to be separable generically from *Pseudaelurus*, although it represents an intermediate stage between that genus (typically) and *Felis*. Nor do I find any reason for removing the American species from *Pseudaelurus*, with the typical species of which they agree more nearly than they do with the types of *Metailurus*."

Stock (1934) summarized the characters of *Metailurus* as follows:—

"*Metailurus* Lower Pliocene. Dentition $\frac{3.1.2.1}{3.1.2.1}$ P^4 with well developed parastyle. M_1 with heel considerably reduced. Diametral index of superior canine, 63.8 (*M. major*), 66.3 (*M. minor*). Anterior end of mandibular ramus without flange or angulation. Condylar and carotid foramina closely connected with foramen lacerum posterius. No alisphenoid canal. Tympanic bulla completely ossified."

Taken together with his list of characters for *Pseudaelurus*, the generic distinction is perfectly clear. *Metailurus* is at present better known than *Pseudaelurus*; though represented by fewer species, they are much more complete than anything known of *Pseudaelurus*. *Pseudaelurus* may be distinguished from *Metailurus* by having 3-4 premolars and on P^4 the parastyle is weak. The progressive trends from *Pseudaelurus* through *Metailurus* to *Felis* are the reduction of the anterior premolars and the reduction of the protocone with corresponding increase in the size of the parastyle on P^4 . The size changes in the upper canine do not appear to follow a definable trend. *Metailurus* represents an intermediate stage morphologically between *Pseudaelurus*

and *Felis* and it seems preferable to retain this generic distinction; *Pseudaclurus* for the European and American species, *Metailurus* for the Asiatic species. This holds true for all but two species, "*Felis*" *leiodon* and *Pseudaclurus africanus*, the latter being discussed below.

A fragment of a right mandibular ramus from Pikermi was described by Weithofer (1888) as "*Felis*" *leiodon*: this has been shown by Thenius (1951) to be conspecific with another mandible from Pikermi described by Hensel (1862) as *Machairodus parvulus*. On the strength of a newly described maxillary dentition from Pikermi, Thenius regarded all Pikermi specimens as generically comparable with *Metailurus minor* from the Chinese Pontian and in consequence has renamed "*Felis*" *leiodon* as *Metailurus parvulus* (Hensel). Teilhard de Chardin (1945: 18-23) referred to "*Metailurus tunggurensis* Colbert 1939, p. 78, fig. 18": this is a mistake for *Metailurus mongoliensis*.

Metailurus africanus (Andrews)

(Pl. 5, fig. 4; Text-figs. 61, 62)

1914 *Pseudaclurus africanus* Andrews: 178-179, pl. 29, figs. 1a, b.

DIAGNOSIS. Dental formula $\frac{3.1.2.1}{7.1.3.7}$; a *Metailurus* intermediate in size between *M. major* and *M. minor*. The anterior process of the nasal bone elongate: upper canine somewhat more ovate than in *M. major*: P^4 paracone and metacone equal length; large maxillary and mandibular canine-premolar diastema; vestigial P_2 present.

HOLOTYPE. M.10634. Left mandibular ramus with I_3 , C, P_{3+4} , from Bed 31 at West Kachuku, Karungu, Victoria Nyanza, Kenya.

ADDITIONAL MATERIAL. M.19076. Facial region of skull, the maxillae with all dental alveoli and P^{3+4} present, described and figured below. From Site 18, Rusinga Island, Kavirondo Gulf, Kenya.

CMF.4001 Isolated P_4 from Songhor.

DESCRIPTION. Most of the anterior of the skull is preserved though much crushed. The premaxilla has a long ascending ramus which probably almost reached the frontal; centrally the anterior palatine foramen is about the same size as the alveolus of I^3 . The convex surface of the maxilla is evidence of the deep roots for the canine tusks. The infra-orbital foramen is drop-shaped, its height being about half the length of the canine alveolus; the lower border of the foramen is situated about 1.5 cms. above the base of the main cusp of P^3 . The nasal bone is long and broad, with a prominent anterior descending ramus overlapping the premaxilla. The frontal bones, though incomplete, suggest a narrow interorbital region: the post-orbital process was short and from its posterior border arises the ridge demarcating the

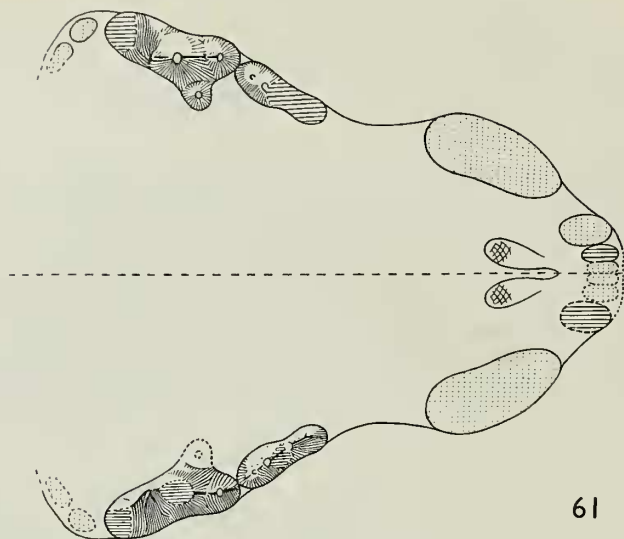
anterior limit of the temporal muscle; this ridge ascends rapidly and meets the sagittal line about 1.5 cms. behind the postorbital process. The jugal is very robust; posteriorly it is broken and cannot be traced beyond the orbit.

P³⁺⁴ are preserved on both sides but only the alveoli of the other teeth remain. The alveolus of I² is slightly larger than that of I¹ and much compressed laterally. The alveolus of I³ is very much larger than that of I², more or less circular, and on the right side contains the tooth root. The three incisor alveoli lie close together in an arc and are separated by a short diastema from the large oval canine alveolus. The canine alveolus measures 16.2 mm. antero-posteriorly and the maximum transverse width is 9.0 mm. The canine is separated from the premolar series by a diastema almost as long as the canine alveolus. There is no trace on either side of any premolar anterior to the bi-rooted P³. The prominent central cusp of P³ has an anterior keel terminating in a small anterior cusp: the posterior half of the central cusp is broken on both teeth: the posterior cusp is larger than the anterior one and a cingulum terminates the tooth posteriorly. In P⁴ the paracone is slightly higher than the metacone and equal to it in length: internally the two cusps are sectorial and externally are separated by a deep trough: the metacone terminates in a ridge, the paracone in a point: the parastyle is in line with the metacone and paracone and is larger than the protocone. The alveolus of M¹ indicates a small bi-rooted tooth lying transversely close behind P⁴.

REMARKS. From the table of measurements on the dentition, *M. africanus* can be seen to be comparable in size with *M. mongoliensis* and *M. parvulus*, and intermediate between *M. major* and *M. minor*. From the alveolus, the upper canine of *M. africanus* appears to have been intermediate in size between *M. major* and *M. minor*, though more ovoid than either of these two species and in this character similar to *M. parvulus*. P³⁺⁴ are proportionately more similar to those of *M. major* than to other species. The equality of paracone and metacone length on P⁴ allies the species to the Chinese forms and differentiates it from *M. parvulus*. The incisor-canine diastema is of similar size in *M. africanus* and *M. major* and much larger in the smaller species *M. minor*. The canine-premolar diastema in *M. africanus* is much larger than that of any other species. The anterior process of the nasal is longer in African species than in either of the two Chinese species.

The holotype mandible described by Andrews fits the above skull perfectly; the size and spacing of the teeth correspond precisely. P₂ in the holotype must have been minute judging from the pinhole alveolus; thus the effective diastema extended from canine to P₃ and the outer concavity of the mandible in this region gave room for the long upper canine when the jaw was closed, a feature better developed in *M. major* than in *M. minor*.

The additional tooth referred to the species (CMF.4001) is a P₃. It measures 5.6 mm. laterally and 11.5 mm. antero-posteriorly. The tooth is indistinguishable in character from P₄ on the holotype, but is slightly smaller; their ratios of length to breadth are identical.



FIGS. 61, 62. *Metailurus africanus* (Andrews). Facial region, distortion corrected.
(61) Occlusal aspect. (62) Lateral aspect. (M.19076), Rusinga Is. $\times 1$.

The stratigraphic distribution of the species of *Pseudaelurus* and *Metailurus* is as follows:

<i>Pseudaelurus quadridentatus</i> Gervais (type species)	Vindobonian, Europe
„ <i>lorteti</i> Gaillard	Vindobonian, Europe
„ <i>transitorius</i> Depéret	Vindobonian, Europe
„ <i>tournauensis</i> (Hoernes)	Vindobonian, Europe
„ <i>marini</i> Villalta & Crusafont	Vindobonian, Europe
„ <i>ailuroides</i> MacDonald	Barstovian, N. America
„ <i>pedionomus</i> MacDonald	Clarendonian, N. America
„ <i>intrepidus</i> Leidy	Barstovian-Clarendonian, N. America
„ <i>marshi</i> Thorpe	Clarendonian, N. America
„ <i>martini</i> (Hibbard)	Hemphillian, N. America
„ <i>kansensis</i> (Hibbard)	Hemphillian, N. America
<i>Metailurus major</i> Zdansky (type species)	Pontian, Asia
„ <i>minor</i> Zdansky	Pontian, Asia
„ <i>parvulus</i> (Hensel)	Pontian, Europe
„ <i>mongoliensis</i> Colbert	Sarmatian, Asia
„ <i>africanus</i> (Andrews)	“Miocene”, Africa

The European *Pseudaelurus* species are all Vindobonian in age and the North American species higher, ranging from the Barstovian to the Hemphillian. The Mongolian species of *Metailurus* is Sarmatian (Tung Gur formation), the Chinese and Pikermi species are all Pontian. *Pseudaelurus* is more primitive, occurs earlier in the stratigraphic record and appears to persist longer than *Metailurus*. The species and distribution of both genera are, however, not sufficiently abundant to enable any firm stratigraphic conclusions to be drawn for the African occurrence, save to suggest that Middle to Late Miocene is likely.

TABLE 10

Measurements (in mm.) on dentitions of *Metailurus*

* = alveolus measured

		<i>Metailurus africanus</i> (Andrews) M.19076 and M.10634 Miocene: Kenya	<i>Metailurus major</i> Zdansky Pontian: China	<i>Metailurus minor</i> No. 3+4 Zdansky Pontian: China	<i>Metailurus mongoliensis</i> AM.26599 Colbert Miocene: Mongolia	<i>Metailurus parvulus</i> ex. Thénier Pontian: Pikermi
I ¹	lat	—	3.0	2.8	—	—
	a-p	—	4.7	3.6	—	—
I ²	lat	3.2*	4.0	3.5	—	—
	a-p	5.0*	5.4	4.3	—	—
I ³	lat	4.8*	6.7	4.8	—	—
	a-p	7.2*	8.2	5.2	—	—
C	lat	9.0*	11.5	7.8	—	6.9*
	a-p	16.2*	18.7	12.3	—	12.9*
P ³	lat	5.7	8.9	6.6	—	6.7
	a-p	13.0	20.2	13.7	—	13.5
P ⁴	lat	10.3	14.0	10.6	—	9.5
	a-p	21.0	31.2	24.0	—	21.4
M ¹	lat	10.0	11.9	10.0	—	9.3
	a-p	3.5	5.5	4.7	—	4.1
I ₁	lat	—	2.7	2.2	2.3	—
	a-p	—	3.3	2.7	2.0	—
I ₂	lat	—	3.8	2.9	3.0	—
	a-p	—	4.2	3.0	2.7	—
I ₃	lat	2.8	5.6	4.1	3.7	—
	a-p	5.9	5.3	3.9	3.3	—
C	lat	5.5	9.0	6.5	7.5	6.6
	a-p	10.1	12.7	8.8	11.5	9.1
P ₃	lat	4.6	8.4	5.3	5.7	—
	a-p	10.1	15.5	9.9	12.0	—
P ₄	lat	6.8	9.3	6.5	6.8	6.5
	a-p	13.9	21.0	14.5	15.0	15.0
M ₁	lat	—	10.1	7.2	7.2	7.0
	a-p	—	23.2	18.1	17.3	17.8
<i>Ratios (lateral/anteroposterior)</i>						
	$\frac{C}{P^3}$.55*	.61	.65	—	.53*
	$\frac{P^4}{P^3}$.44	.44	.48	—	.50
	$\frac{P^4}{M^1}$.49	.45	.44	—	.44
	$\frac{M^1}{P^3}$.35*	.46	.47	—	.44
	$\frac{C}{P_3}$.54	.71	.74	.65	.72
	$\frac{P_4}{P_3}$.45	.54	.53	.47	—
	$\frac{P_4}{M_1}$.49	.44	.45	.45	.43
	$\frac{M_1}{P_3}$	—	.43	.40	.42	.39
<i>Diastemae</i>						
	$\frac{I^3-C}{C-P^3}$	4.4	4.3	6.2	—	—
	$\frac{C-P^3}{C-P_3}$	13.0	5.8	3.4	—	3.7
	$\frac{C-P_3}{C-P_3}$	20.8	18.5	8.4	5.5	7.2

III. CONCLUSIONS AND THE AGE OF THE FAUNA

The carnivores do not reveal much about the environment, being predators mainly dependent on the herbivores in the fauna. They range from very small species about the size of a stoat to the large hyaena-like *Pterodon*. The picture of forests on the volcanic slopes, swamp with gallery type vegetation and savannah with flash floods is well described by Chesters (1957) and by Bishop (1963).

The carnivores described in this paper are recorded from nine localities. Two of these, Rusinga and Napak, are subdivided into a number of sites and these are quoted where known; unfortunately many of the best finds were made on Rusinga before site designation was initiated. Rusinga Island, Mfwanganu Island and Karungu in western Kavirondo are associated with the Rangwa volcanic centre. Ombo is a high level site in eastern Kavirondo. Songhor and Koru are in Nyanza, east of the Kavirondo Gulf and associated with the Tinderet volcanic centre. Moruorot is in the Northern Frontier District of Kenya and Napak in Karamoja, Uganda. Kaboor is in Turkana, Northern Kenya.

Age analysis can be based on three lines of evidence; the relationships of the carnivores to other carnivore faunas, the deductions obtained for other faunal elements and radiometric dating of the fossiliferous tuffs.

TABLE II
Distribution of the carnivores by sites

	Fayūm	Napak	Moruorot	Mfwanganu	Rusinga	Karungu	Ombo	Maboko	Songhor	Koru	Kaboor	Elizabethfeldern
<i>Kelba quadeemae</i>		+		+	+							
<i>Teratodon spekei</i>									+	+		
<i>Teratodon enigmae</i>									+			
<i>Anasinopa leakeyi</i>				+	+	+		+				
<i>Metasinopa napaki</i>		+										
<i>Dissopsalis pyroclasticus</i>											+	
<i>Metapterodon kaiseri</i>					+	+						+
<i>Metapterodon zadoki</i>					+							
<i>Pterodon africanus</i>	+	+			+							
<i>Pterodon nyanzae</i>					+		+					
<i>Leakitherium hiwegi</i>					+							
<i>Hyaenodon andrewsi</i>	+		+		+		+		+			
<i>Hyaenodon matthewi</i>					+				+			
<i>Hyaenodon pilgrimi</i>					+				+			
<i>Hecubides euryodon</i>		+		+	+				+	+		
<i>Hecubides macrodon</i>					+							
<i>Kichechia zamanae</i>		+	+	+	+				+			
<i>Metailurus africanus</i>					+	+			+			

The carnivore evidence for stratigraphical dating can be summarized for individual genera. *Kelba*, if an arctocyonid, has its closest relationships among the Palaeocene and Eocene arctocyonids of North America, which have two late survivors in the Lower Oligocene of Mongolia. *Teratodon* finds closest comparison with *Quercytherium* from the Phosphorites du Quercy (Upper Eocene to Middle Oligocene) of France. *Anasinopa* is comparable with *Sinopa* and *Tritemnodon* from the Middle Eocene of North America and Europe, and is more primitive than *Metasinopa* from the Fluvio-marine Series (Sannoisian, Lower Oligocene) of the Fayûm, Egypt, the latter genus being also known from Napak I. The *Dissopsalis* species from Kaboor is closely comparable with *D. carnifex* from the Chinji Stage (probably Middle Miocene) of India. *Metapterodon* from Karungu and Rusinga is also known from Southwest Africa and Stromer (1926) on the basis of this and other faunal elements suggested a similar age for both deposits. *Pterodon africanus* is known from the Kavirondo sites and from the Sannoisian of the Fayûm. The genus *Hyaenodon* ranges in Europe from Upper Eocene to Upper Oligocene, with more restricted ranges in Asia and North America; one species, *H. andrewsi* is common to the Sannoisian of the Fayûm and to East Africa. *Hecubides* may be regarded as a primitive 'Amphicyon'; this form genus is recorded from the Middle Oligocene to Late Miocene (Stampian-Pontian). The non-African species of *Hecubides* are *H. lemanensis* from the Aquitanian of France and *H. americanus* from Nebraska (horizon unknown). *Kichechia* is a herpestine, the subfamily being recorded from Upper Oligocene times in Europe. *Metailurus africanus* is closely comparable with two Pontian species from China. The evidence is thus equivocal, the creodonts suggesting Oligocene and the fissipeds Miocene dating; since they are of holarctic origin the creodonts might be expected to survive later in Africa and this is borne out by the novel character of the fauna. If a single age is required by other evidence, then Lower Miocene is most likely.

Proboscideans and anthracotheres are useful mammalian taxa in comparative age analyses. Andrews (1914) designated a Lower Miocene (Burdigalian) age to the Karungu deposits on the basis of the close affinity of *Deinotherium hobleiy* with *D. cuvieri* from France. The association of a small species of *Deinotherium* with *Gomphotherium angustidens* in the Kavirondo is also well known outside Africa from the Burdigalian deposits of Sables de l'Orleanais, France; El Papiol, Spain; Kotyháza, Hungary and Bugti Hills, Baluchistan. *G. angustidens* occurs at all these sites and the *Deinotherium* species are virtually indistinguishable. Most of the sites also contain anthracotheres comparable with East African species, but carnivores are poorly represented, usually by *Amphicyon* fragments. Burdigalian faunas have been identified in other parts of Africa. In Southwest Africa Stromer (1926) found no proboscideans or anthracotheres, but the carnivore, hyracoid and lagomorph elements support his argument for comparison with Kavirondo sites. The Moghara site, west of Cairo, yielded *G. angustidens* but no *Deinotherium* and only one carnivore (*Hyaenaelurus*) (Fourtau 1920). At Gebel Zeltan in Central Libya *Deinotherium hobleiy* occurs in association with *Gomphotherium angustidens*, anthracotheres, hyaenodont, felid and canid carnivores (Savage 1965). Recently the two probos-

cideans have been found at new sites in Algeria and Tunisia. All this evidence strengthens the case for a late Burdigalian age for the East African faunas, at least in part.

	PALAEOCENE	EOCENE	OLIGOCENE	MIOCENE	PLIOCENE
<i>Arctocyonidae</i> (for <i>Kelba</i>)	—————		----		
<i>Quercytherium</i> (for <i>Teratodon</i>)		-----	-----		
<i>Sinopa</i> (for <i>Anasinopa</i>)		—			
<i>Metasinopa</i>			●		
<i>Dissopsalis</i>				●-----	
<i>Pterodon</i>		—————	▲		
<i>Hyaenodon</i>		—————	▲		
<i>Amphicyon</i> (for <i>Hecubides</i>)			●	—————	
Herpestinae (for <i>Kichechia</i>)			—————	—————	—————
<i>Metailurus</i>				●	
<i>Pseudaelurus</i>				—————	

TABLE. 12. Stratigraphic range of genera or nearest taxon where *genera nova*. Broken line where record doubtful. ● Stratum with closely comparable species. ▲ Stratum with identical species.

Both Chesters (1957) and Verdcourt (1963) emphasised the uniformity and modernity of the flora and mollusca throughout the succession, supporting the concept of a single biotic assemblage. This evidence, while not directly useful in dating, does not necessarily conflict with the Burdigalian estimate.

The fauna of Maboko (=Kiboko) Island in the Kavirondo Gulf has been stated to be of two ages; Hopwood (in Shackleton 1951) argued for Burdigalian and Helvetian ages on the basis of the proboscideans; Leakey (*in* Whitworth 1958) suggested Vindobonian or Pontian for the younger elements. Recent discoveries by Leakey (1961) at Fort Ternan, a site associated with the Tinderet volcanic centre as are Songhor and Koru, suggest the fauna is of Pontian age.

Radiometric dating of rock samples using K-A₄₀ is not yet complete. Preliminary results for Napak I give 19 million years (Bishop 1964); for the basal (Kiahera) series on Rusinga Island 15.3 and for Fort Ternan 14 million years (Evernden et al 1964). The Napak figure would be consistent with a late Burdigalian age. The Rusinga figure seems too young, but the sample gave ages ranging from 15.3 to 167 million years and may not have been from the Kishara Series.

My current assessment is that more than one fauna is represented in the Kenya-Uganda Tertiary sites; that one of these is Burdigalian in age with numerous sites in east and west Kavirondo and in Karamoja. A younger fauna is present at Fort Ternan; there is a hint of a post-Burdigalian fauna at Maboko and Kaboor, and possibly at Rusinga, Songhor and Karungu, mainly on basis of *Metailurus* and *Dissopsalis*. For the younger fauna a Vindobonian (Middle Miocene) and or Pontian (Upper Miocene) age is probable.

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